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A REVISION OF THE FERN GENUS PELLAEA SECTION PELLAEA\*

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The species included in this section of *Pellaea* are predominately Cordilleran growing in dry, rocky habitats under semi-desert conditions quite unlike those usually associated with ferns. These and most other ferns of arid regions in the New World belong to the tribe Cheilantheae of the Polypodiaceae. The revision of this section was undertaken as part of a program of study on this tribe. In the 'Genera Filicum', Copeland recognizes the genus *Pellaea* as a natural one although his remarks on the affinities of the group do not entirely support that view. A more pessimistic regard toward *Pellaea* as a genus is evident in the view of Thomas Moore some fifty years earlier for he considered it as a medley of pteroids, cheilanthes and platylomas and stated—"Pellaea can only be kept up as a kind of botanical refuge for the destitute."

The section PELLAEA is a restricted but natural group based on vegetative morphology such as the nearly glabrous, imparipinnate blade and free venation, and on the continuous marginal indusium and terminal sori on discrete vein ends. Relationships with *Doryopteris*, *Notholaena* and *Cheilanthes* are not wholly clear and the final disposition of the group in *Pellaea* and with other related genera is best delayed until the entire complex can be reviewed.

The entities included in section PELLAEA under the above provisions number 15 species and 5 varieties. Within this small group there appears to be two types of speciation. Apomixis, polyploidy and hybridization have influenced speciation in *P. globella*, *P. sagittata* and *P. ovata*. The series related to *P. ternifolia* seems to have evolved through gradual quantitative differentiation and through isolation of resulting populations.

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## GEOGRAPHY AND ECOLOGY

The species prevail in the southwestern United States and Mexico. *P. rufa* in South Africa is the only species belonging to this section which occurs in the Old World. Three species are confined to the United States; one is endemic in Chile and two in Mexico. Ten of the species or varieties occur in the southwestern United States and Mexico and three of these, *P. ternifolia*, *P. ovata* and *P. sagittata*, are distributed along the Cordillera to Argentina. The Cordilleran distribution pattern is similar to other ferns as *Notholaena sinuata*, the *N. nivea-incana* group, the *Cheilanthes pyramidalis-marginata* group and to the Umbellifers *Osmorhiza mexicana* and *Sanicula liberta*. The most extensive distribution among the pellaeas is that of *P. ternifolia* in the western highlands of the Americas from Texas to Argentina, in the Sierra de la Ventana in eastern Argentina, and it is reported by C. H. Hicken<sup>1</sup> from Minas Geraes although I have seen no specimens from Brazil. Both *P. ternifolia* and *P. ovata* occur in Hispaniola but the former is unique in the group in its occurrence in the Hawaiian Islands as well. The Cordilleran-Hawaiian distribution is also common to *Asplenium monanthes*. The genus occurs in Africa but within this section only the Chilian *P. myrtillifolia* and Californian *P. andromedaefolia* have a close relationship with *P. rufa* of the south African Karroo.<sup>2</sup> Floristic relationships between California, Chile and South Africa occur in other genera as *Acaena* in Rosaceae and *Menodora* in Oleaceae.

The southwestern United States and adjacent Mexico is the most probable center of dispersal of these species, for the ranges of all but *P. Brewerii* and *P. glabella* either converge in this region or seem to be derivatives of those that do. In two species complexes it is possible to detect the derived types by the number of spores per sporangium and in these the ranges of the ancestral members converge in this same region.

In the eastern United States the most common species is *P. atropurpurea* which ranges from Guatemala to Florida, Vermont and Colorado with two isolated stations in British Columbia and in the vicinity of Lake Athabasca in Saskatchewan. The species is reported to be a triploid and apogamous by both Manton<sup>3</sup> and Britton.<sup>4</sup>

*Pellaea atropurpurea*, *P. glabella*, *P. ovata* and *P. sagittata* var. *cordata* are calciphilous while *P. ternifolia* and related species are reported mainly from igneous rock. Both *P. ternifolia* var. *ternifolia* and *P. sagittata* var. *cordata* occur on the lava beds in the vicinity of Mexico City. The former grows directly on the lava while the latter occurs in crevices and pockets, where soil has accumulated, along with other calciphiles as *Ophioglossum Engelmannii* and *Selaginella Wrightii*. *P. ternifolia* appears to tolerate a variety of habitats and a range in altitude of 200-4000 meters. Wiggins<sup>5</sup> reports it and also *P. sagittata* and *P. ovata* on the dry,

<sup>1</sup> Soc. Argent. de Cien. Nat. 13:206. 1916.

<sup>2</sup> Ann. Mo. Bot. Gard. 42:101. 1955.

<sup>3</sup> Manton, I. Prob. Cytol. & Evol. of the Pterid. Cambridge Univ. Press. 1950.

<sup>4</sup> Britton, D. M., University of Maryland, Dept. of Horticulture, personal correspondence.

<sup>5</sup> Amer. Fern Journ. 36:1. 1946.

earthen walls of Ecuadorian towns. *P. ovata* is also an epiphyte on trees and generally has a subscendent habit with fronds nearly 1½ m. long.

#### MORPHOLOGY

These species are not fern-like in aspect and their leaf design is undoubtedly influenced by the arid conditions in which they grow. The spores and gametophyte have remarkable tolerance to desiccation. Herbarium specimens two to five years old bore spores which were germinated in ten days. Prothallia of *P. longimucronata* were kept air-dry for two months at temperatures ranging from 80 to 100° F. and became green when watering was resumed although no sporophytes were produced. Pickett and Manuel<sup>6</sup> carried on some experiments on desiccation of prothallia and sporelings of *P. atropurpurea* and *P. glabella* in which some plants were air-dry for nine and some for 18½ months. When watering was resumed some of the plants became green and continued growth. After five years Pickett<sup>7</sup> examined the same cultures and 5 per cent showed whole or partial recovery when satisfactory growing conditions were restored.

The rhizomes grow deep in crevices or under rocks and contain an oily substance which is still present in specimens collected some forty years ago. The rhizome has two general forms—one relatively massive, up to 1 cm. in diameter, compact or somewhat elongate, multicapitular and ascendent or decumbent—the other slender, cord-like, less than ½ cm. in diameter, creeping and with buds on the older portions. The vascular system of the rhizome is not a solenostele in the strict sense but approaches a dictyostele. There may be more than one foliar gap in a section of the slender and long-creeping stems and there may be several in compact stems with short internodes.

The scales of the rhizome are mostly elongate-lanceolate or elongate-triangular with a more or less filiform and tortuous apex and entire or dentate margins. Young scales are usually concolorous. Mature scales may be concolorous or bicolorous with a central dark, sclerotic stripe or basal portion. In a few species scales of the older portions of the rhizome are wholly sclerotic, brown and lustrous except for a narrow, clear border. Cells of the scale base are usually small, squarish or irregular and above they are usually 20 or more times longer than broad. Bands of constricted cells are frequent in *P. glabella* and seem to occur where the scales are appressed. Scales of the stipe base are generally similar to those of the rhizome although in *P. sagittata* the stipe and bud scales are exceptionally broad and pseudopeltate.

The plants are generally stiff and erect in habit and the fronds are coriaceous in texture. The smallest mature plants have pinnate fronds 1 cm. long and the largest are quadripinnate, up to 125 cm. long, and may be subscendent. The leaves are usually monomorphic although several species have the segments of the fertile fronds somewhat contracted. This latter condition is especially evident in

<sup>6</sup>Bull. Torr. Bot. Club 53:1-5. 1926.

<sup>7</sup>Amer. Fern Journ. 21:49-56. 1931.

*P. atropurpurea*. The blade is usually elongate-triangular but is linear in *P. Breweri* and *P. ternifolia*. The blade of *P. ovata* is most elaborate with many divisions and strongly flexuous axes. In the series of species from *P. ternifolia* to *P. mucronata* a relationship exists in the pinna between the relative position of the terminal segment and the lateral segments adjacent to the rachis. The pinna has a simple, ternate form in *P. ternifolia*, is longer and has more segments in *P. longimucronata* and still more complex in *P. mucronata*. In each of these species, irrespective of the development of the pinnae, the lateral segments nearest the rachis are inclined toward the terminal segment. *P. mucronata* having the most complex pinna-form also occupies a peripheral position in the geographic range of the series and it seems possible that this is a derived form in which the blade has been elaborated.

The form and indument of the bud and the type of vernation are distinctive in some of the species. *P. atropurpurea* has lanate buds which are elongate and become uncoiled soon after they arise from the rhizome. The buds of *P. glabella* var. *glabella* are round, tightly coiled, sparsely pubescent and slowly uncoil. The stipe may be plane or sulcate on the upper surface or it may be terete. Stipe color is castaneous to black or straw colored to ruddy brown. A few species have stipes essentially light colored with dark patches. In transverse section the stipe has a single vascular bundle having the form of a flattened or sharp angled V with inrolled ends. In *P. Breweri* and *P. glabella* the fronds articulate at the stipe base. The blade is imparipinnate but not entirely so in *P. Breweri* and some specimens of *P. glabella*.

The manner in which the pinnae depart from the rachis is a useful character in distinguishing *P. atropurpurea* and *P. glabella*. In the former the pinna-rachises depart abruptly from the rachis and form broad angles while in the latter they are somewhat decurrent or adnate to the rachis below the axis and form smaller, acute angles with the rachis. The length of the pinna-rachises ranges mostly between 5 and 10 cm. but this may be up to 15 cm. in *P. ovata* and *P. andromedae-folia* or in some species it is lacking.

Venation is pinnate, free, rarely anastomosing and is usually obscure being sunk in the mesophyll. The sunken stomates give a punctate texture to the lower surface of the segments. The receptacle occupies the vein end usually less than  $\frac{1}{5}$  of the distance to the midvein and is clavate or cuneate in form. If the sporangia are abundant the sori are superficially coalescent but the vein ends are free or rarely two are fused.

The indusium is formed by the reflexed margin of the segment which may be only slightly or strongly inrolled. The tissue which functions as the indusium is usually membranaceous but may be essentially unmodified.

The sporangia stalks are as long or longer than the capsules except in *P. Pringlei* and *P. brachyptera* where they are short. The annulus is vertical, amber colored or rarely yellow and does not extend to the insertion of the stalk. In some apogamous species the annulus may be oblique or rarely a cluster of cells at the capsule apex.

Simple capitate trichomes occur in *P. brachyptera* and *P. mucronata* and occasionally in *P. longimucronata* and *P. ternifolia* var. *Wrightiana*. They are found among the sporangia and secrete a whitish yellow substance. In an old paper the chemical nature of an apparently similar substance in *Pityrogramma triangularis* is noted by Blasdale<sup>8</sup> in relation to the material found in *Notholaena*, *Cheilanthes* and *Primula*. In *Pityrogramma triangularis* the substance is called Ceroptene and consists of yellow, triclinic crystals and whitish amorphous bodies melting at 135° C. and soluble in both alcohol and xylol.

Spore color in the species with dark stipes is tan to brownish and the rugae are scarcely prominent with the exception of *P. atropurpurea*. The latter, along with the light striped species, has prominently ornamented spores which are generally light yellow. The spores are of special interest in this group for those of apogamous strains are larger, usually monolete with 32 per sporangium in contrast to the smaller, usually trilete 64 spored non-apogamous strains. The spores remain viable for a few years; thus it is possible to germinate them and check the gametophyte state of recent herbarium specimens. A positive indication of apogamy is shown by prothallia on which sporophytes are formed subsequent to the production of antheridia although no archegonia are formed.

#### CYTOTOLOGY

The chromosome counts in this work may be regarded as preliminary until additional material is available to support them. The cytology, however, has been helpful in indicating some of the mechanisms by which these ferns reproduce and has facilitated the taxonomic disposition of several entities. In a survey of the chromosome numbers of ferns of eastern North America, Dr. Donald M. Britton<sup>9</sup> of the University of Maryland treated *P. glabella* var. *glabella* and he kindly agreed to do additional counts on related species of *Pellaea*. He has studied ten members of six species from aceto-carmine squashes of the spore mother cells and these are reported in the treatment of the species. The chromosome base number of  $n = 29$  has been established and both triploids and tetraploids have been formed on this base. From their morphology the triploids *P. atropurpurea* and *P. sagittata* var. *sagittata* appear to be allopolyploids. *P. ternifolia* has both diploid and polyploid strains and it is possible that the latter may be a parent in the triploid *P. atropurpurea*.

#### PHYLOGENY

Since polyploidy is prevalent in the group it is difficult to plot relationships until chromosome counts are reported for all species. There is likewise difficulty in the establishment of primitive and advanced characters. A sequence of genera based on the receptacular condition within the tribe Cheilantheae is discussed by R. M. Tryon<sup>10</sup> in his treatment of *Doryopteris*. He regards this genus as most advanced and derived from either a Cheilanthoid or Pellaeoid stock and *Pellaea* as

<sup>8</sup> Erythea 1:252. 1892.

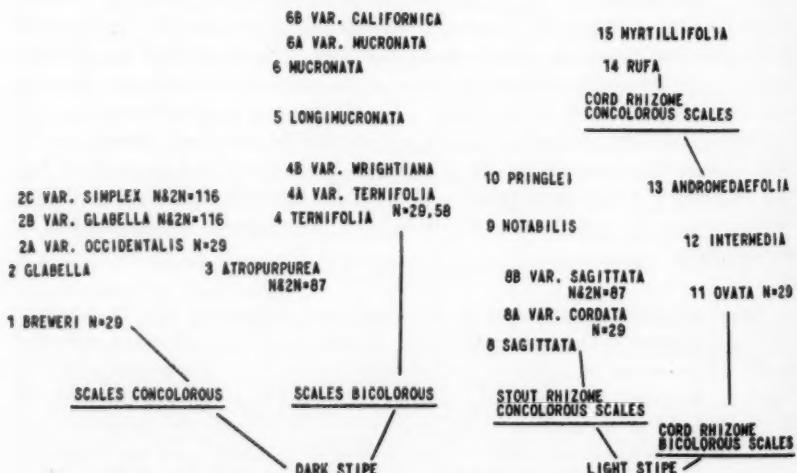
<sup>9</sup> Amer. Journ. Bot. 40:575-583. 1953.

<sup>10</sup> Contrib. Gray Herb. No. 143. 1942.

parallel to or derived from *Cheilanthes* or *Notolaena* and perhaps intermediate to these and *Doryopteris*.

Within the section *PELLAEA* several natural lines are apparent. Two of these are distinguished on the basis of the color of the stipes. Dark colored stipes are considered advanced since some of the light stiped species have less specialized, creeping rhizomes. Within the dark stiped group there are two distinct lines. One line composed of *P. Breweri* and *P. glabella* has evidently emerged from a Cheilanthonoid stock as shown in the decurrent pinnae and the pinnate-pinnatifid division of the blade. The other line of dark stiped species is the most closely related group of the section. It appears to have evolved from *P. ternifolia* and is of such continuity that some difficulty is encountered in delimiting the species. These seem to have evolved through morphological and ecological adaptations such as those discussed by Mason<sup>11</sup> in his paper on the role of plant geography in taxonomy in reference to the tribe *Helenieae* in the southwestern United States. The lack of distinctive characters in these Compositae is interpreted as an indication of relatively recent elaboration. Among the species of *Pellaea* with light stipes those with cord-like rhizomes are considered more primitive and of these *P. ovata* is most specialized by its elaborate frond. Of the light stiped species having stout, multicapitital rhizomes *P. sagittata* is regarded more specialized by its dimorphic scales. *P. notabilis* seems to be intermediate between the two main groups for although the stipes are essentially light colored their bases are dark. It is most closely related to *P. atropurpurea* on several characters.

#### 7 BRACHYPTERA



Phyletic chart of *Pellaea* section *PELLAEA* with known chromosome numbers.

<sup>11</sup> Chronica Botanica 14:154-159. 1953.

The phyletic chart shows the relationships discussed above and the chromosome counts that have been reported.

#### BACKGROUND OF THE STUDY

From Linnaeus to Desvaux's 'Prodrome' of 1827, six of the entities included here were placed in *Pteris*, one of the major fern genera of earlier botanical works. As interest in ferns increased the botanical gardens of Europe developed their living collections which included many from the American continents and fern classification advanced. This group was recognized as a natural genus twice within the year 1841 and thus the nomenclature has been confused from the beginning. Link<sup>12</sup> proposed *Pellaea* from the collections at the Berlin Gardens and John Smith<sup>13</sup> applied the name *Platyloma* for the same group from the collections at Kew Gardens. Smith's name, published in August, appears to have preceded that of Link. Alston has noted in the British Museum's copy of Link's work that it was issued between September 3 and 10, fide—Aag. Bibl. f. Deutsch. Lib. No. 37 p. 421. 1841. A committee on nomenclature for Pteridophytes<sup>14</sup> reported a unanimous vote to conserve *Pellaea* and Dr. Pichi-Sermoli,<sup>15</sup> Secretary of the Committee, has reviewed the matter. The International Code adopted by the 8th Congress at Paris, 1954, includes *Pellaea* among the genera to be conserved.

Presl<sup>16</sup> took up a still earlier name, *Allosorus* of Bernhardi and treated these species in section MONOMORPHI along with species now referred to *Jamesonia*, *Doryopteris* and *Cheilanthes*. Otto Kuntze<sup>17</sup> follows Presl in order to avoid conflict with *Pellia* of Raddi and *Pella* of Gaertner and since he believed Presl's work more adequate than Link's.

Fée<sup>18</sup> distributed these species among four of six groups, based largely on the shape of the blade, he includes in *Pellaea*.

W. J. Hooker<sup>19</sup> also considered vegetative characters as diagnostic for he arranged these species in *Pellaea* according to the division of the blade. His diagnosis of the species, illustrations and general information on the collections he examined are better than previous accounts.

Prantl<sup>20</sup> proposed the section EUPELLAEA for these species as one of eight sections and indicated that these are the *Pellaea* of Link. He considered the condition of the blade, the sori, the vascular system and scales. Diels<sup>21</sup> essentially followed Prantl's scheme.

<sup>12</sup> Fil. Sp. Hort. Bot. Berol. Cult. 59. 1841.

<sup>13</sup> Journ. Bot. ed. W. J. Hooker 4:160. 1841.

<sup>14</sup> Taxon 3:70. 1954.

<sup>15</sup> Webbia 9:428. 1953.

<sup>16</sup> Tent. Pterid. 131. 1836.

<sup>17</sup> Rev. Gen. Pl. 2:802. 1891.

<sup>18</sup> Gen. Fil. 128. 1850-52.

<sup>19</sup> Sp. Fil. 2:130-153. 1885.

<sup>20</sup> Engl. Bot. Jahrb. 3:415. 1882.

<sup>21</sup> Engl. & Prantl, Nat. Pflanzenfam. 14:266. 1899.

Until studies of the African pellaeas and other genera of the Cheilantheae are completed the disposition of this group as a section of *Pellaea* seems the most practicable course.

#### USE AND CULTIVATION

These neat, novel plants were popular in English stoves and American conservatories during the Victorian era. Two of the plants were introduced for greenhouses by Messrs. Veitch & Sons of Chelsea who obtained them from California. They were described as species and the types at Kew are nursery specimens more robust than the native Californian plants. *P. brachyptera*, *P. ovata*, *P. andromedaefolia* and *P. mucronata* were included in the florist trade of the period and the last is described as a handsome house plant producing as many as 75 fronds. Many of the species are now grown in botanical collections for they are easily cultivated. W. J. Hooker noted that several of the pellaeas were cultivated in the temperate fern houses at Kew more than a hundred years ago and at present the hanging baskets of *P. ovata* and *P. sagittata* in these fern houses are most attractive. Several of the Mexican pellaeas are grown in the University of California greenhouses and *P. ternifolia* var. *ternifolia* was volunteering there in pots of cacti and succulents. Seven species have been grown in the experimental greenhouse at the Missouri Botanical Garden. The plants require little special care other than a rock substrate and good drainage. *P. atropurpurea*, an attractive rock garden plant, is evergreen and does especially well on native limestone.

There are a few references on the medicinal uses of *Pellaea*. *P. mucronata* is reported to make a palatable beverage recommended for the kidneys and as a blood purifier. The vernacular name *Tea Fern* and the Tejon Indian name *Calagula* have been applied. Chilean miners use the name *Coca* or *Yerba Coca* for the local *P. myrtillifolia* and prepare an infusion of it taken to allay pain.

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I am indebted to the curators of the herbaria of the following institutions for the generous loan of specimens: Chicago Natural History Museum, Gray Herbarium, Muséum National d'Histoire Naturelle, Paris, Naturhistoriska Riksmuseum, Stockholm, Naturhistoriska Riksmuseum Paleobotanical Department, Stockholm, New York Botanical Garden, United States National Museum, University of British Columbia, University of California, Cornell University, University of Kansas, University of Michigan, University of Minnesota, University of Utah, State College of Washington, Pullman, University of Washington, Seattle, University of Wyoming and Yale University. The abbreviations for these and other herbaria are taken from 'Index Herbariorum,' part I (Regnum Vegetabile vol. 2) compiled by Lanjouw and Stafleu.

I wish to thank Mr. F. Ballard of Kew, Mr. J. A. Crabbe of the British Museum, Mme. Tardieu-Blot of Paris, and Mr. C. V. Morton of the United States National Herbarium for courtesies extended during the course of this study. Prof. Maximino Martínez of the Herbario Nacional del Instituto de Biología, Universidad Nacional

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I am especially grateful for collections of living plants which were received from Dr. E. F. Castetter of the University of New Mexico, Dr. Seville Flowers of the University of Utah, Dr. G. B. Ownbey of the University of Minnesota and Mr. J. W. Thompson of Seattle.

Dr. Donald M. Britton of the University of Maryland has done the chromosome studies which are reported in this treatment. The information has been incorporated in the taxonomy and phylogeny of the group. A more detailed account of the cytology and evolution of these ferns is in preparation by Dr. Britton and myself.

I am indebted to Mrs. Bernadette Velick who has helped me in the preparation of the drawings.

For his patient council and kindly criticism I am most grateful to my husband, Rolla M. Tryon, under whose guidance this study has been made.

#### SYNOPSIS

*PELLAEA* Link, Fil. Sp. Hort. Bot. Berol. 59. 1841, nom. conserv. Section *PELLAEA*.

*Eupellaea* Prantl, Engl. Bot. Jahrb. 3:415. 1882.

The natural characters of the group are best expressed in the imparipinnate, usually coriaceous blade; continuous marginal indusium; terminal sori on discrete and usually clavate vein ends; stipe and rachis tan to black, usually glabrous, smooth, without wings or conspicuous scale scars; costa of the segments mostly obscure; sporangia usually long stalked; spores yellowish tan to brown, smooth or rugose.

Although the section is not defined by a few striking characteristics it is a relatively homogeneous one. Among the species listed below some may not conform in all respects but are most properly placed here on the sum of their characters.

Type species: *Pellaea atropurpurea* (L.) Link.

Species: 1. *P. breweri* D. C. Eaton, 2. *P. glabella* Mett. ex Kuhn, 2A. var. *occidentalis* (E. Nelson) Butters, 2B. var. *glabella*, 2C. var. *simplex* Butters, 3. *P. atropurpurea* (L.) Link, 4. *P. ternifolia* (Cav.) Link, 4A. var. *ternifolia*, 4B. var. *Wrightiana* (Hook.) A. F. Tryon, 5. *P. longimucronata* Hooker, 6. *P. mucronata* (D.C. Eaton) D. C. Eaton, 6A. var. *mucronata*, 6B. var. *californica* (Lemmon) Munz & Johnston, 7. *P. brachyptera* (Moore) Baker, 8. *P. sagittata* (Cav.) Link, 8A. var. *cordata* (Cav.) A. F. Tryon, 8B. var. *sagittata*, 9. *P. notabilis* Maxon, 10. *P. Pringlei* Davenp., 11. *P. ovata* (Desv.) Weatherby, 12. *P. intermedia* Mett. ex Kuhn, 13. *P. andromedaefolia* (Kaulf.) Fée, 14. *P. rufa* A. F. Tryon, 15. *P. myrtillifolia* Mett. ex Kuhn.

The position of *Pellaea Bridgesii* Hook., which in its general aspect resembles some of the species treated here and occurs mainly in California, remains a problem. I have excluded it on the basis of the conduplicate segments lacking reflexed margins, the short stalked sporangia which are borne on an elongated receptacle one quarter to one half the distance to the costa and which persist in a cup-like

form after dehiscence. It resembles some species of *Notholaena* in the length of the receptacle and in the abundant waxy indument produced among the sporangia.

#### KEY TO SPECIES

- a. Stipe and rachis castaneous to black; spores usually with a sparsely rugose exospore. b.
- b. Scales of the rhizome concolorous; stipe and rachis terete or elliptical. c.
- c. Fronds monomorphic; pinnae sessile or the stalks somewhat decurrent on the rachis and arising at acute angles to the rachis; stipe and rachis glabrous or sparsely pubescent; scales of the rhizome discrete, a uniform rust-brown color. d.
- d. Rhizome massive with numerous compressed, short, articulated stipe bases; mature fronds with rachises mostly green in the terminal portion of the blade, the apical segments strongly decurrent; the basal pinnae without persistent stalks often sessile or subsessile. 1. *P. Breweri*, p. 135
- d. Rhizome moderately stout with few stipes persistent, these more or less spreading; mature fronds with rachises mostly brownish in the terminal portion of the blade, the apical segments somewhat decurrent or stalked; the basal pinnae with persistent stalks. 2. *P. glabella*, p. 138
- c. Fronds dimorphic; pinnae stalked, not decurrent and arising at broad angles to the rachis; stipe and rachis scurfy with appressed pubescence; scales of the rhizome matted, rust colored with the young tips light tan. 3. *P. atropurpurea*, p. 144
- b. Scales of the rhizome bicolorous with a sclerotic central stripe or base; stipe and rachis sulcate, convex or plane on the upper surface. e.
- e. Segments with opaque whitish borders, usually membranaceous; sporangia long stalked. Oklahoma to Utah southward to Argentina, Dominican Republic, Hawaiian Islands. f.
- f. Basal pinnae usually less than twice as long as broad, entire or divided into 3–11 segments; the pinnae-rachises up to 2 cm. long. 4. *P. ternifolia*, p. 149
- f. Basal pinnae usually more than twice as long as broad, divided into 9–21 segments; the pinnae-rachises up to 7 cm. long. 5. *P. longimucronata*, p. 155
- e. Segments entirely green, the border undifferentiated or narrow, lutescent green; sporangia short stalked. Southern Oregon, California, Baja California. g.
- g. Ultimate segments of the basal pinnae shorter than the pinna-rachis; blade ovate-triangular to rhomboid; pinnae ovate-linear. 6. *P. mucronata*, p. 157
- g. Ultimate segments of the basal pinnae longer than the pinna-rachis; blade linear; pinnae semi-circular. 7. *P. brachyptera*, p. 162

- a. Stipe and rachis straw colored to ruddy brown or darker at the base and mottled above; spores usually with a prominent rugose exospore. h.
- h. Rhizome moderately stout, compact; scales of the stipe base and buds tawny, broad, cordate or pseudo-peltate; fronds approximate; spores sparsely rugose. 8. *P. sagittata*, p. 164
- h. Rhizome usually slender, cord-like and creeping, or moderately stout and compact; scales of the stipe base and buds tan, rust colored or brown, slender, acicular to lanceolate-triangular; fronds distant or approximate; spores prominently rugose. i.
- i. Blades usually once or twice pinnate; pinnae with 1–3 segments; segments elongate-lanceolate or lobed (stellate to ternate). j.
- j. Veins, except for the midvein, obscure; pinnae elongate-lanceolate, several times longer than broad, subcoriaceous. Nuevo León and Tamaulipas. 9. *P. notabilis*, p. 170
- j. Veins evident; pinnae stellate to ternate, nearly as long as broad, chartaceous or herbaceous. Central and western Mexico.
10. *P. Pringlei*, p. 172
- i. Blades tri-quadripinnate or more highly divided; pinnae generally with 10–50 segments; segments mainly ovate. k.
- k. Rachis and pinna-rachises strongly flexuous. 11. *P. ovata*, p. 174
- k. Rachis and pinna-rachises straight. l.
- l. Mature rhizome scales bicolorous. Southwestern United States and Mexico. m.
- m. Veins obscure; segments coriaceous; buds pubescent. Texas, New Mexico, Arizona and northern Mexico.
12. *P. intermedia*, p. 177
- m. Veins visible on the lower surface of the segments; segments herbaceous; buds paleaceous. California.
13. *P. andromedaefolia*, p. 179
- l. Mature rhizome scales concolorous. Chile, South Africa.
- n. Rhizome cord-like, long-creeping; spores essentially smooth. South Africa. 14. *P. rufa*, p. 184
- n. Rhizome moderately stout, compact; spores rugose. Chile.
15. *P. myrtillifolia*, p. 184

1. **PELLAEA BREWERI** D.C. Eaton, in Proc. Amer. Acad. 6:555. 1865. (Lectotype: *Brewer 2038* YU!, Isotypes: MO! NY!, Paratypes: *Brewer 1919, 2102* YU!, Photo of Holotype and Paratypes: GHI! US!) Fig. 1. Map 1.

*Allosorus Breweri* (D.C. Eaton) O. Ktze. Rev. Gen. Pl. 2:806. 1891.

Rhizome compact, ascendent, massive with many compressed bases of articulated stipes. Scales of the rhizome entangled or matted, uniform rust brown, these and those of the base of the stipes concolorous, lustrous, acicular, flexuous, the margins sinuate, not dentate, the cells of the scale base short, rectangular or with oblique end walls, the apex attenuate. Fronds 2.5–21.0 cm. long, bent

or arcuate, monomorphic, the buds with sparse, reddish brown pubescence. Stipe and rachis terete, often flat when dry, sparsely pubescent, castaneous, lustrous, becoming darker and dull with age, the stipe with prominent lines of articulation, readily breaking at right angles to the axis, the rachis green at the apex. Blade 1.5 cm. long and 0.5 cm. broad to 16.0 cm. long and 3.5 cm. broad, linear-oblong, once pinnate or pinnate-pinnatifid, pure green, subglaucous, the pinnae of nearly the same length, departing at acute angles to the rachis, the upper pinnae entire, sessile, usually strongly decurrent on the rachis, the lower pinnae deeply 2-lobed, unilateral or mitten-shaped, rarely 3-lobed, subsessile or with short, green, rarely brown stalks, decurrent, the axils usually green, without pinna-rachises. Segments 0.5 cm. long and 0.3 cm. broad to 2.5 cm. long and 1.0 cm. broad, linear-ovate to deltoid, usually lobed, herbaceous, the border narrow, whitish, crenulate, the apex muticous. Sporangia sessile or subsessile, the annulus pale yellow, rarely amber colored. Spores 64 per sporangium, tetrahedral-globose, dark to light brown, with a scarcely prominent rugose exospore.

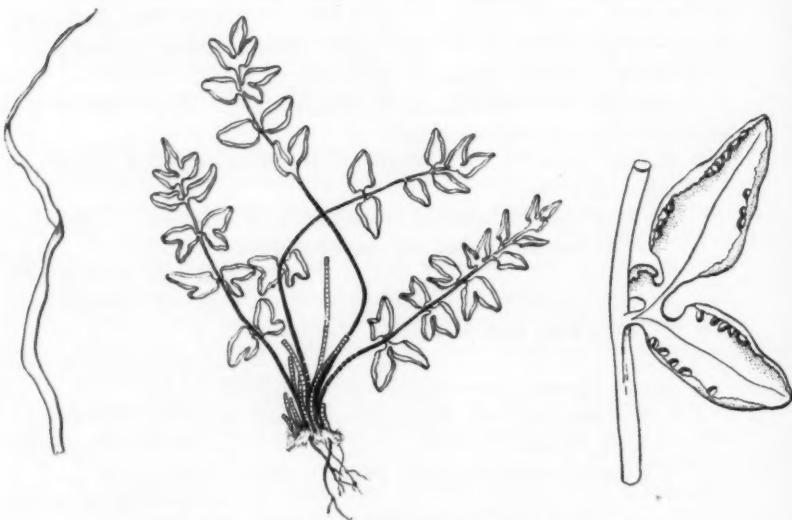
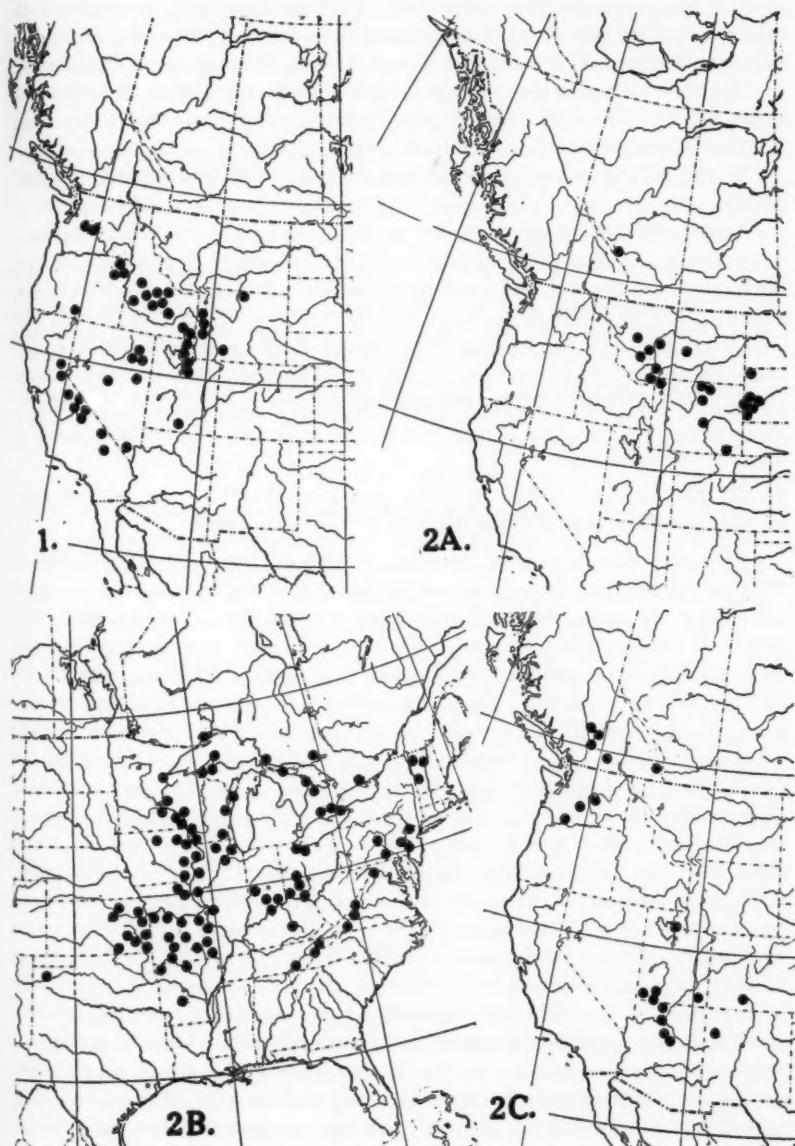


Fig. 1. *Pellaea Breweri*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

*P. Breweri* resembles *P. glabella* more than any other member of the genus and a relationship exists here between *Pellaea* and several Mexican and South American species of *Cheilanthes*. In *P. Breweri* and *P. glabella* the division and lobing of the frond, the position and attachment of the pinnae on the rachis and the articulation of the stipes are more like those of *Cheilanthes Brandegii*, *C. allosuroides*, *C. pyramidalis* and *C. marginata* than other *pellaes*.

The mature fronds of *P. Breweri* articulate at constricted bands on the stipe. No special tissue is developed in the stipe but the hypodermis and cortex are com-



1. Distribution of *Pellaea breweri*.

2A. Distribution of *Pellaea glabella* var. *occidentalis*, 2B. var. *glabella*, 2C. var. *simplex*.

posed of relatively large, thin-walled cells. Fractures occur from the center of the stipe outward, possibly due to the mechanical strain set up by the drying of the delicate central tissue. This is also evident in *P. glabella*, particularly var. *occidentalis*.

The chromosome number reported by Dr. D. M. Britton is  $n = 29$  from specimens collected by Seville Flowers, Salt Lake County, Utah, Big Cottonwood Canyon, Wasatch Mountains, on July 25, 1953.

Usually on granite rocks or basalt but also reported from limestone, at 1600-3800 m.

Representative specimens:

UNITED STATES. WYOMING: M. & R. P. Ownbey 1878 (GH, MO, NY, WS); Williams & Pierson 834 (GH, MO, US). IDAHO: Hitchcock & Mulick 11004 (NY, US, WS, WTU); Thompson 14022 (GH, MO, US, WTU). UTAH: July 25, 1953, S. Flowers (MO); Goodding 1114 (MO, US); Maguire et al. 13153 (GH, MO, US, WS). NEVADA: Clokey 7815 (MO, US, UT, WS, WTU); S. Watson 1361 (GH, US, YU). WASHINGTON: Thompson 7832 (US), 9515 (GH, NY, MO, US, WS, WTU). OREGON: Coville & Leiberg 301 (US); Thompson 13220 (GH, NY, MO, US, WS, WTU). CALIFORNIA: Alexander & Kellogg 3103 (MO, US, WS); Bolander 6243 (GH, MO, US, YU); Among rocks at Ebbets Pass, Aug. 4-16, 1863, Brewer 2038, 2102 (NY, YU); Duran 2811 (GH, MO, NY, US, WTU).

2. *PELLAEA GLABELLA* Mett. ex Kuhn, in Linnaea 36:87. 1869. (Lectotype: Specimen cited from Kimmswick, near St. Louis, Mo. B?).

Rhizome moderately stout, compact, decumbent or ascendent, multicarpital. Scales of the rhizome discrete and usually not matted, uniform rust brown, these and those at the base of the stipes concolorous, lustrous, linear, flexuous, often with horizontal bands of constricted cells, the margins sinuous or with broad irregular teeth, the cells of the scale base small, squarish, or elongate with oblique end walls, the apex somewhat attenuate, more or less tortuous, discrete, not entangled. Fronds 1-36 cm. long, usually lax, arcuate or sinuous, monomorphic, the buds sparsely pubescent. Stipe and rachis terete, glabrous or nearly so, castaneous, lustrous, becoming darker and dull with age, the stipe breaking at right angles to the axis, occasionally with perpendicular lines of articulation, the rachis castaneous or greenish at the apex. Blade 0.75 cm. long and 0.5 cm. broad to 21 cm. long and 8 cm. broad, linear or ovate-lanceolate, once to twice pinnate, clear or bluish green, glaucous or subglaucous, the lower pinnae less than twice as long as the upper, departing at acute angles to the rachis, the upper pinnae entire or auriculate, sessile or subsessile, the lower pinnae entire, 2-5 lobed or once pinnate with 3-7 segments, stalked, the pinna-stalks somewhat decurrent, the axils colored as the rachis, the pinna-rachises up to 5 cm. long. Segments 0.5 cm. long and 0.3 cm. broad to 3.5 cm. long and 1.0 cm. broad, oblong to linear-ovate, usually lobed or auriculate, herbaceous to subcoriaceous, the border narrow, whitish, crenulate, the apex muticous to submucronate. Sporangia with long or short stalks, the annulus amber colored, occasionally oblique. Spores 32 or 64 per sporangium ellipsoidal or tetrahedral-globose, occasionally dumbbell-shaped, rusty brown, the exospore sparsely to moderately rugose.

In his studies of *P. glabella*, Butters segregated two western species on the

basis of differences in frond size, shape of the pinnae and vascular bundle and the size of the spores.<sup>22</sup> The size and number of spores per sporangium are of interest here for they reflect cytological differences. Britton<sup>23</sup> reports the chromosome number of *P. glabella* var. *glabella* from southern Ontario as  $n = 116$  and considers this to be a tetraploid on the base number of 29. The plants are apogamous and the sporangia are 32 spored. He reports a tentative count of *P. glabella* var. *simplex*, collected by J. W. Thompson 17246 from Grant Co., Washington, as also  $n = 116$  and the material is 32 spored and apogamous. The monoploid number predicted in the above counts is realized in *P. glabella* var. *occidentalis*. Specimens collected by G. B. & F. Ownbey 1676 from Laramie Hills, Albany Co., Wyoming, have 64 spored sporangia, a normal sexual development and the chromosome count was determined as  $n = 29$ . Thus the 116 numbered members may be considered as tetraploids derived, at least in part, from *P. glabella* var. *occidentalis*.

On rocks or cliffs, in crevices, usually on limestone, rarely on granitic rocks.

Arizona north to southern British Columbia and northeast across the United States to Vermont.

#### KEY TO VARIETIES

- Spores 64 per sporangium; fronds 1–15 cm. long, once pinnate, the pinnae with 2 or 3 lobes, usually sessile or with stalk and rachis up to 0.2 cm. long. Alberta to Wyoming and South Dakota. 2A. var. *occidentalis*, p. 139
- Spores 32 per sporangium; fronds 1–36 cm. long, once to twice pinnate, the pinnae deeply lobed or with 3–7 segments, with stalk and rachis up to 5.0 cm. long.
- Fronds 4–36 cm. long, the basal pinnae persistent, with stalk and rachis up to 5.0 cm. long. Vermont to Minnesota and Texas. 2B. var. *glabella*, p. 141
- Fronds 1–20 cm. long, the basal pinnae usually withered, with stalk and rachis up to 1.0 cm. long. British Columbia to Washington and Utah to New Mexico. 2C. var. *simplex*, p. 142

2A. *PELLAEA GLABELLA* var. *occidentalis* (E. Nelson) Butters, in Amer. Fern Journ. 7:82. 1917. Fig. 2A. Map 2A.

*Pellaea atropurpurea* var. *occidentalis* E. Nelson, in Fern Bull. 7:30. 1899. (Holotype: A. Nelson 1919! RM!, Isotype: MO! NY!).

*Pellaea pumila* Rydb. in Mem. N. Y. Bot. Gard. 1:4. 1900. (Holotype: Rydberg 1101 NY!, Isotype: US!).

*Pellaea occidentalis* (E. Nelson) Rydb. loc. cit. 466. 1900.

Rhizome slender, somewhat ascendent. Scales of the rhizome and base of the stipes sinuate or the margins with few blunt teeth or erose, the cells of the base of the scales squarish. Fronds 1–15 cm. long. Stipe usually with perpendicular lines of articulation. Blade 0.75 cm. long and 0.5 cm. broad to 10 cm. long and 4 cm. broad, once pinnate or pinnate-pinnatifid, bluish green. Segments ovate to oblong,

<sup>22</sup> Amer. Fern Journ. 7:77. 1917; 11:39 75. 1921.

<sup>23</sup> Amer. Journ. Bot. 40:575. 1953.

mostly entire or 2- or 3-lobed and mitten-shaped, those of the basal pinnae withering early with persistent petiolules, the apex muticous, rarely submucronate. Sporangia stalks equal to the capsule length. Spores 64 per sporangium, mostly tetrahedral-globose, the exospore with short, moderately prominent rugae.

Generally these are smaller plants than the others of the *P. glabella* group but not conspicuous in any unique structure. Within the geographic range of the species they occupy a central position, mostly discrete and more restricted than the other varieties. As mentioned in the discussion of *P. atropurpurea* the possibility exists that hybrids were produced between that species and *P. glabella* var. *occidentalis* producing the eastern var. *glabella* and the western var. *simplex*. The ranges of *P. atropurpurea* and var. *occidentalis* are contiguous in the Black Hills of South Dakota and nearly so in the vicinity of Banff, Alberta. A few specimens from the former region appear intermediate. *P. glabella* var. *occidentalis* is undoubtedly the source from which the polyploid members of the complex have been derived either through hybridization or possibly autoploidy.

In narrow fissures of limestone ledges at 1300–2800 m.

Banff, Alberta, southeast in the United States to Wyoming and the Black Hills of South Dakota.

Representative specimens:

CANADA. ALBERTA: Aug. 14, 1920, Butters (US); Ulke 901 (NY).

UNITED STATES. MONTANA: Blankenship 638 (MO, RM, US); Suksdorf 463 (GH, WS). WYOMING: L. C. Anderson 648 (UTC); Laramie Hills, June 13, 1896, Aven Nelson 1919 (MO, NY, RM); A. & E. Nelson 6837 (GH, MO, NY, US); G. B. & F.



Fig. 2A. *Pellaea glabella* var. *occidentalis*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

1957]

## TRYON—PELLAEA SECTION PELLAEA

141

*Ownbey 1676* (MO). SOUTH DAKOTA: *Palmer 37126* (GH, MO); Bull Springs, limestone district west of Custer, Black Hills, July 27, 1892, *Rydberg 1191* (GH, NY, US).

2B. *PELLAEA GLABELLA* var. *glabella*

## Fig. 2B. Map 2B.

*Pellaea atropurpurea* var. *Bushii* Mack. ex Mack. & Bush, Man. Fl. Jackson Co., Mo., 5. 1902. (Holotype: *Mackenzie 447* NY!, Isotype: RM!).

*Cassebeera atropurpurea* var. *minima* Eggert ex Farw. in Amer. Midl. Nat. 12:281. 1931. (Holotype: Eggert, July 1878 MICH!).

*Pellaea atropurpurea* var. *minima* Eggert ex Farw. loc. cit. 1931, in synon.

*Cassebeera atropurpurea* var. *glabella* (Mett. ex Kuhn) Farw. loc. cit. 1931.

*Pellaea atropurpurea* f. *glabella* (Mett. ex Kuhn) Clute, Our Ferns, 109, 386. 1938.

Rhizome moderately stout, decumbent. Scales of the rhizome and base of the stipes sinuate or the margins with irregular, broad teeth, the cells of the base of the scales mostly elongate with oblique end-walls. Fronds 4–36 cm. long. Stipe occasionally with perpendicular lines of articulation. Blade 2 cm. long and 1 cm. broad to 21 cm. long and 8 cm. broad, once to twice pinnate, bluish green. Segments oblong-lanceolate, entire or auriculate or 3–5 lobed, persistent, the apex submucronate. Sporangia stalks as long or shorter than the capsule. Spores 32 per sporangium, ellipsoidal or tetrahedral-globose, the exospore with sparse, scarcely prominent rugae.

Variety *glabella* appears to represent a genotype both vigorous and well adapted to the arid, limestone ledges which it occupies in the central and eastern United States. It is generally distinguished from the western varieties by its larger size.



Fig. 2B. *Pellaea glabella* var. *glabella*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale; section of the rachis with pinna-stalks.

As indicated in the discussion of *P. atropurpurea*, *P. glabella* var. *glabella* is similar in several respects although the two can be distinguished by several characters as follows:

*Pellaea glabella* var. *glabella*

Leaves monomorphic.  
Leaves lax, arcuate or sinuous, 4–36 cm. long.  
Blades linear to elongate-ovate.  
Stipe and rachis glabrous or with few bicolorous hairs.  
Pinnae at acute angles to the rachis, somewhat decurrent, departing gradually (fig. 2B).  
Basal pinnae with 3–7 segments; less than twice as long as the upper pinnae.  
Scales of the rhizome discrete, uniformly rust-brown, lustrous, the tips not entangled.  
Margins of the fertile segments usually strongly reflexed with relatively few sporangia exposed.

*Pellaea atropurpurea*

Leaves dimorphic.  
Leaves erect, straight, stiff, 6–50 cm. long.  
Blades elongate-triangular.  
Stipe and rachis hispid, scurfy.  
Pinnae at broad angles to the rachis and departing abruptly (fig. 3).  
Basal pinnae with 3–15 segments; usually 2 or more times as long as the upper pinnae.  
Scales of the rhizome appressed, matted, dull tawny to rust colored, the young tips tan and entangled.  
Margins of the fertile segments plane with abundant sporangia exposed.

On limestone, calcareous sandstone or dolomite cliffs or bluffs in shaded crevices or exposed ledges at less than 400 m.

Northwestern Texas to the north shore of Lake Superior, Ontario, and east to Tennessee and Vermont.

Representative specimens:

CANADA. ONTARIO: Soper & Burcher 2074 (GH, MO); Taylor et al. 115 (US). UNITED STATES: VERMONT: 1903, Baxter (MO); Fellows 481 (US). PENNSYLVANIA: Aug. 1920, Wherry & Pretz (US). NEW JERSEY: Mackenzie 4621 (MO). WEST VIRGINIA: Sept. 1937, Spawn (US). VIRGINIA: Adams & Wherry 2257 (GH); Wood 3644 (GH). OHIO: Roth et al. 670 (US); Camp 1053 (NY). KENTUCKY: Aug. 1938, Richards (US). TENNESSEE: Jamison & Shaver 4161 (MO); Underwood & Sharp 2523 (MO). MICHIGAN: Hagenab 1157 (US); Aug. 1892, Wheeler (RM, US). INDIANA: R. M. & P. F. Tryon 4348 (MO, US). ILLINOIS: Evers et al. 671 (GH). MINNESOTA: M. F. & J. W. Moore 13563 (MIN, MO). IOWA: Anderson (Pl. Exsicc. Gray. 902) (GH, MO, NY, RM, US, WS). MISSOURI: Bush 2837 (GH, MO, NY, US); Near St. Louis, July, 1878, Eggert (MICH); Limestone rocks at Swope Park, Sept. 13, 1901, Mackenzie 447 (NY, RM). ARKANSAS: May, 1923, Buchholz (MO, US). NEBRASKA: Nov. 1895, Williams & Wilcox (US). KANSAS: Horr E463 (RM, US, UT, WS). TEXAS: D. S. & H. B. Correll 13085 (MO).

2C. *PELLAEA GLABELLA* var. *SIMPLEX* Butters, in Amer. Fern Journ. 7:84, 1917. (Holotype: Heacock 272 GH!, Photo: MO!, Isotypes: MO! NY!).

Fig. 2C. Map 2C.

*Pellaea Suksdorffiana* Butters, in Amer. Fern Journ. 11:40. 1921, based on *P. glabella* var. *simplicior* Butters.

*Pellaea atropurpurea* var. *simplex* (Butters) Morton, in Leaf. West. Bot. 6:156. 1951.

Rhizome moderately stout, ascendent. Scales of the rhizome and base of the stipes sinuate or irregularly dentate, the cells of the base of the scales squarish or with oblique end walls. Fronds 1–20 cm. long. Stipe rarely with perpendicular lines of articulation. Blade 1.0 cm. long and 0.8 cm. broad to 14.0 cm. long and

4.5 cm. broad, usually once pinnate or pinnate-pinnatifid, or occasionally twice pinnate, clear green. Segments oblong-lanceolate, 3–5 lobed frequently with 2 or more small auricles, segments of the basal pinnae withering early with persistent petiolules, the apex muticous or submucronate. Sporangia long stalked, the annulus often oblique. Spores 32 per sporangium, ellipsoidal or tetrahedral-globose occasionally dumbbell-shaped, the exospore with sparse, scarcely prominent rugae.



Fig. 2C. *Pellaea glabella* var. *simplex*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

The distribution of var. *simplex* is discontinuous, occurring in southern British Columbia to southern Washington and in northern Utah to central Arizona and northern New Mexico with a gap in the intervening states. In the few specimens available there is no apparent morphological differentiation between collections from the two isolated areas. In the discussion of *P. atropurpurea* it is suggested that this disrupted distribution may be due to the independent hybrid origin of *P. glabella* var. *simplex* in the two isolated regions where the ranges of *P. atropurpurea* and *P. glabella* var. *occidentalis* were contiguous.

On dry limestone or sandstone cliffs or ledges at 900–3000 m.

British Columbia, Washington, Utah, Arizona, New Mexico, Colorado.

Representative specimens:

CANADA. BRITISH COLUMBIA: Carbonate Draw, Selkirk Mts., July 14, 1904, Heacock 272 (GH, MO, NY); Taylor & Lewis 172 (MO, Univ. B.C.); J. W. & E. M. Thompson 362 (MO, NY, US, WS, WTU).

UNITED STATES. WASHINGTON: Cliffs along the Columbia river, Aug. 11, 1892, *Sukkendorf* 2038 (MO, NY, US, WTU). UTAH: *Rydberg & Garrett* 9421 (NY, RM, US, UT). ARIZONA: *Collom* LJC13 (US); *Tracy* 267 (YU). COLORADO: *Lorew*, Wheeler Exped. 1873 (YU). NEW MEXICO: 1883, *Mathews* (GH).

3. *Pellaea atropurpurea* (L.) Link, Fil. Sp. Hort. Bot. Berol. 59. 1841.

Fig. 3. Map 3.

*Pteris atropurpurea* L. Sp. Pl. 2:1076. 1753. (Holotype: *Clayton* 682, Point-look-out on the Rappahannock river, Va. BM). The Clayton collection was not found at the British Museum; a single frond, collected by Kalm, in the Linnean Herbarium is *P. atropurpurea*.

*Pteris thalictroides* Muhl. "Ind. Fil. Lancast." in Trans. Amer. Phil. Soc. 3:182. 1793, nom. nud., not *P. thalictroides* (L.) Sw. 1801.

*Asplenium atropurpureum* (L.) Bernh. in Schrad. Neu. Journ. 1<sup>2</sup>:10. 1806.

*Pteris spiculata* Schkuhr, Krypt. Gewäch. 1:92, t. 100. 1809. (Lectotype: t. 100, loc. cit.).

*Pteris atropurpurea* var. *venosa* Pursh, Fl. Am. Sept. 2:668. 1814. (Holotype: t. 101, Schkuhr, Krypt. Gewäch.).

*Pteris atropurpurea* var. *punctata* Pursh, Fl. Am. Sept. 2:668. 1814. (Holotype: t. 100, Schkuhr, Krypt. Gewäch.). It is apparent from Schkuhr's text and figures that the table numbers are reversed in Pursh's reference to that work.

*Allosorus atropurpureus* (L.) Kze. ex Presl, Tent. Pterid. 153. 1836.

*Platyloma atropurpurea* (L.) Sm. in Journ. Bot. ed. W. J. Hooker 4:160. 1841.

*Nothochlaena atropurpurea* (L.) Keyserl. Polyp. Cyath. Herb. Bung. 30. 1873.

*Pellaea atropurpurea* var. *cristata* Trel. in Rep. Mo. Bot. Gard. 12:34. 1901. (Holotype: Pauls, Missouri, in 1899, MO!).

*Pellaea atropurpurea* var. *venosa* (Pursh) Gilb. List N. Amer. Pterid. 18. 1901.

*Pellaea atropurpurea* f. *bifida* Hahne, in Fern Bull. 12:117. 1904, nom. nud.

*Pellaea atropurpurea* f. *furcata* Hahne, in Fern Bull. 12:117. 1904, nom. nud.

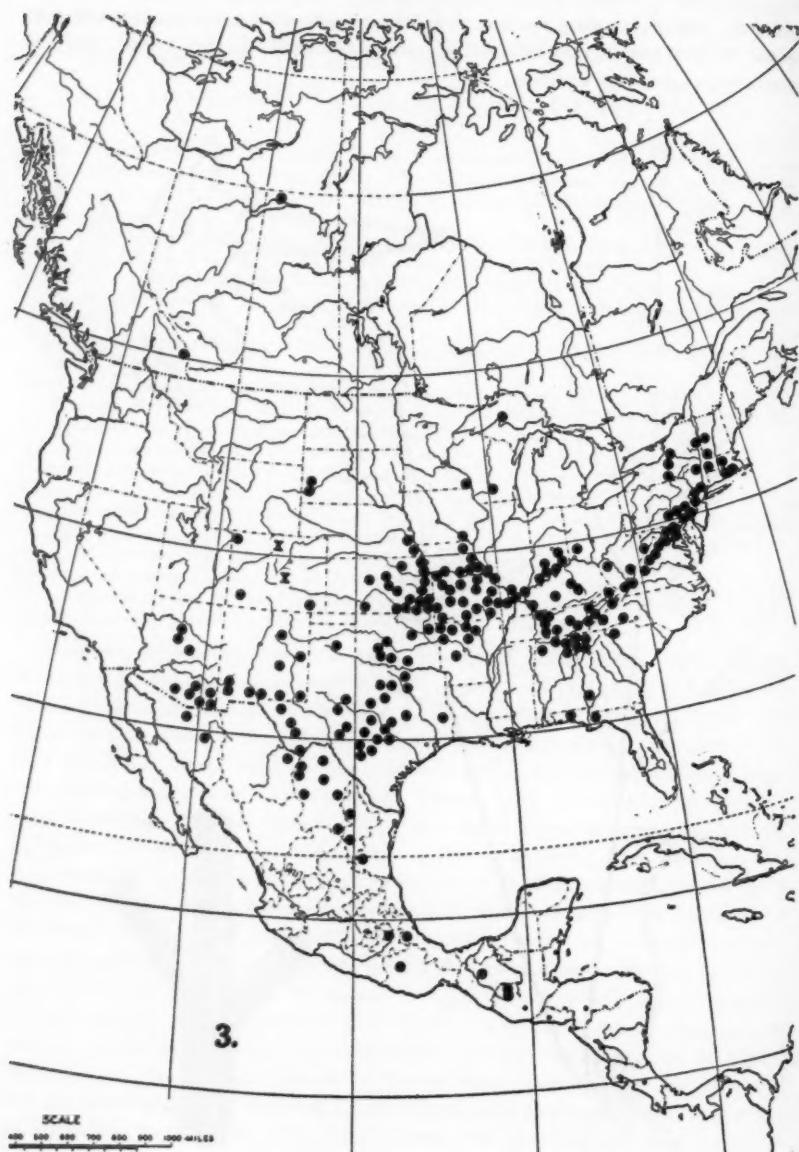
*Cassebeera atropurpurea* (L.) Farw. in Amer. Midl. Nat. 12:281. 1931.

Rhizome moderately stout, compact, decumbent, multicarpital. Scales of the rhizome appressed and matted, rust colored in mass with the young tips light tan, these and those at the base of the stipes concolorous, tawny to rust colored, dull, linear-subulate, usually straight, the margins more or less dentate, the cells of the scale base small, mostly with oblique end walls, the apex attenuate, filiform, somewhat tortuous, appressed and entangled. Fronds 6–50 cm. long, erect, straight, stiff, dimorphic, the buds lanate. Stipe and rachis terete or elliptical, strongly pubescent to hispidulous, atropurpureous to black becoming gray with age, the stipe breaking irregularly, without perpendicular lines of articulation, the rachis of the mature frond atropurpureous to the terminal pinna. Blade 5.0 cm. long and 1.5 cm. broad to 25 cm. long and 18 cm. broad, elongate-triangular, once to tripinnate, clear to dark green, the lower pinnae usually 2 or more times as long as the upper, departing at broad angles to the rachis, the upper pinnae usually entire, subsessile or short stalked, the lower pinnae entire, deeply 1–3 lobed, or usually once pinnate with 3–15 segments, stalked, the pinna-stalks abruptly departing, not decurrent, the axis tan, the pinna-rachises up to 12 cm. long. Segments 1.0 cm. long and 0.5 cm. broad to 7.5 cm. long and 1.0 cm. broad, lanceolate or linear-oblong, entire or auriculate or ternately lobed, subcoriaceous, the undersurface often pubescent along the veins, the border broad, white or often opaque, crenulate, the fertile segments revolute, the apex muticous or mucronate, the mucro 0.25–1.50 mm.

long, flat, with a whitish margin contiguous with that of the segment. Sporangia with long stalks exceeding the length of the capsule, the annulus amber colored. Spores 32 per sporangium, ellipsoidal, rarely dumbbell shaped, yellow, with a prominent, rugose-lacy exospore.



Fig. 3. *Pellaea atropurpurea*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale; section of rachis with pinna-stalks.



3. Distribution of *Pellaea atropurpurea* — X, literature records, see text.

*P. atropurpurea* is widely distributed throughout the eastern United States and wherever it grows it is usually found in abundance. I have observed the species at several stations in New England, Indiana, Minnesota, Texas and Missouri and while much variation exists in frond size the form is essentially uniform. Specimens transplanted from Gray Summit, Missouri, growing in the greenhouse over a period of three years, are more luxuriant than field specimens. These plants produced copious spores which were easily sown, and although only antheridia were produced, sporelings developed. In the eastern United States *P. atropurpurea* often grows on the same rocks or ledges as *P. glabella* var. *glabella* and although the two are readily distinguished when closely observed their relationship has been in question. The cytological and morphological data indicate the possibility of hybrids produced between *P. atropurpurea* and *P. glabella* var. *occidentalis*. The former, apogamous with 87 chromosomes, crossed with the normal sexual *P. glabella* var. *occidentalis*, may have given rise to *P. glabella* var. *glabella* to the east and *P. glabella* var. *simplex* to the west. Both of these varieties of *P. glabella* have chromosome numbers of 116 and are apogamous. Some morphological comparisons of the four entities are made in the following chart. It might be expected that the hybrids would bear a stronger resemblance to *P. atropurpurea* from which they would receive a triple genome.

	<i>P. atropurpurea</i>	<i>P. glabella</i> var. <i>glabella</i>	<i>P. glabella</i> var. <i>simplex</i>	<i>P. glabella</i> var. <i>occidentalis</i>
Frond length	6–50 cm.	4–36 cm.	1–20 cm.	1–5 cm.
Lines of articulation on the stipe	None	Occasionally	Rarely	Abundant
Pubescence on stipe and rachis	Abundant bicolorous hairs, hispid	Sparse bicolorous hairs	Sparse bicolorous hairs	Glabrous or rarely with bicolorous hairs
Length of pinna-stalk and rachis	Up to 120 mm.	Up to 50 mm.	Up to 10 mm.	Usually sessile, rarely up to 2 mm.
Number of segments per pinna	3–15	3–7	3–5	1 — this may be 2–3 lobed

A remark by Butters<sup>24</sup> in his studies of the pellaeas in the western United States pertaining to *Pellaea glabella* var. *occidentalis* is appropriate here ". . . it stands at one extreme of a series and *P. atropurpurea* at the opposite extreme".

From a morphological survey of the species in section PELLAEA, *P. atropurpurea* appears to be more closely related to *P. ternifolia* and *P. notabilis* which occur in Mexico. *P. atropurpurea* very probably originated from such an austral source and has spread to the north and east across the United States and into Canada.

<sup>24</sup> Amer. Fern Journ. 7:82. 1917.

Cytological studies on the group seem to support the morphological evidence on the relationships between *P. atropurpurea* and *P. ternifolia*. Dr Irene Manton<sup>25</sup> reports a chromosome count of  $n & 2n = 87$  for *P. atropurpurea* which is interpreted as a triploid pending the existence of a monoploid relative with 29 chromosomes. Dr. Britton confirms this report of 87 for *P. atropurpurea* from material collected by myself at Gray Summit, Missouri. He also reports counts of both  $n = 29$  and  $n = 58$  for *P. ternifolia*.

On exposed or shaded ledges and crevices of limestone cliffs, masonry walls or rocky loam of forest floor, at 300–3200 m.

Guatemala, northward in Mexico along Sierra Oriental, northeast across the United States to Vermont with outlying stations in the Black Hills of South Dakota, Keweenaw Point on Lake Superior, southeastern British Columbia and on the north shore of Lake Athabasca, Saskatchewan. Some of the specimens from the last two localities are depauperate but can be identified on the basis of the branching of the pinna-rachises, the slender, attenuate scales, prominent ornamentation of the spores and the long basal pinnae.

Two literature records from Colorado, indicated on the map by X, are taken from W. A. Webber in University of Colorado Studies, Biology Series No. 3:68. 1955.

#### Representative specimens:

CANADA. BRITISH COLUMBIA: *Eastham* 11068 (MO, WTU, Univ.B.C.). SASKATCHEWAN: *Raup* 6558 (CU, GH).

UNITED STATES. VERMONT: *Faxon* in 1877 (GH, NEBC). MASSACHUSETTS: *Bissell* in 1906 (GH, YU). CONNECTICUT: *Barnhart* 603 (NY). RHODE ISLAND: *Greenman* 2503 (MO). NEW YORK: *Eames* 9016 (MO, US). NEW JERSEY: *Griscom* 4817 (MO). PENNSYLVANIA: *Heller* 711 (MO, US). DISTRICT OF COLUMBIA: *Maxon* 6303 (GH, MO, NY). MARYLAND: 1896, *Waters* (US). VIRGINIA: *Adams* & *Wherry* 2265 (MO, US). WEST VIRGINIA: *Allard* 3592 (GH, NY, US). NORTH CAROLINA: *Oosting* 35318 (MO, US). SOUTH CAROLINA: *Davis* in 1912, (MO). GEORGIA: *Harper* 353 (GH, MO, NY); *Tborne* & *Muenscher* 7685 (CU, UC). FLORIDA: *Small* & *Knight* in 1934 (GH, NY, US). ALABAMA: *D. S.* & *H. B. Correll* 8284 (GH, NY, US). OHIO: *Demaree* 11472 (MO). MICHIGAN: *Fernald* & *Pease* 3035 (GH, NY, US). INDIANA: *Tryon* 4439 (GH, MO, NY, US). KENTUCKY: *Palmer* 17842 (GH, MO); *Smith* et al. 3443 (GH, NY, US). TENNESSEE: *Pollard* & *Maxon* 417 (GH, US). ILLINOIS: *Tryon* 4052 (MO). MINNESOTA: *Schuster* A5009 (MIN). MISSOURI: *Bush* 5353 (GH, MO, US); 1899, *Eureka*, *Pauls* (MO); *Steyermark* 65394 (F). ARKANSAS: *Palmer* 6904 (MO, US). SOUTH DAKOTA: *Degener* & *Peiler* 16701 (NY, US); *Ryderberg* 1190 (GH, US). NEBRASKA: *Webber* Herb. in 1889 (MO). KANSAS: *Horr* E459 (GH, KANU, US). OKLAHOMA: *Houghton* 3528 (GH, MO, NY). TEXAS: *Moore* & *Steyermark* 3550 (GH, MO, US); *Mueller* 8266 (GH, MO, NY, US). COLORADO: *Rogers* 4070 (US). NEW MEXICO: *Maguire* et al. 11653 (GH, US). ARIZONA: *Phillips* 2799 (MO).

MÉXICO. CHIAPAS: *Ghiesbreght* 216 (F, GH, YU). CHIHUAHUA: *Stewart* 2475 (GH). COAHUILA: *Stanford* et al. 391 (MO, US); *Wynd* & *Mueller* 358 (GH, MO, NY). NUEVO LEÓN: *C. H.* & *M. T. Mueller* 362 (GH, US). PUEBLA: *Arseña* 3548 (GH, MO, US). OAXACA: *Conzatti* 1912 (F), 4279 (US). SONORA: *Hartman* 357 (GH, NY, US). TAMAULIPAS: *Stanford* et al. 943 (MO, US). VERACRUZ: *Bourgeau* 3068 (GH, NY).

GUATEMALA. HEUHEUTENANGO: *Standley* 62598 (F, US), 82761 (F).

<sup>25</sup> Manton, I. Prob. Cytol. and Evol. of the Pterid. Cambridge Univ. Press, 1950.

4. *PELLAEA TERNIFOLIA* (Cav.) Link, Fil. Sp. Hort. Bot. Berol. 59. 1841.

Rhizome moderately stout, elongate, decumbent, multicarpital. Scales of the rhizome appressed, scarcely entangled, brownish or the tips tan, these and those at the base of the stipes usually bicolorous with a narrow sclerotic stripe, subulate, straight or falcate, the margins usually irregularly dentate or erose, the cells of the scale base small, irregular, those above many times longer than broad, the apex attenuate, filiform, appressed and scarcely entangled. Fronds 4–50 cm. long, erect, straight and stiff, monomorphic, the buds sparsely pubescent, rarely lanate. Stipe and rachis convex or plane on the upper surface or sulcate, rarely terete, glabrous or rarely pubescent, glaucous, castaneous becoming darker with age, to ebony black, the stipe breaking irregularly without articulation lines, the rachis of the mature frond black or castaneous to the terminal pinna. Blade 3.0 cm. long and 0.5 cm. broad to 32 cm. long and 6 cm. broad, linear, lanceolate or elongate-triangular, once or bipinnate, clear or grayish green, the pinnae of nearly the same length or the lower longer, departing at broad angles to the rachis, entire, ternate, or with 3–11 segments, subsessile or stalked, pinna-stalks not decurrent, the axes colored as the rachis or tannish, the pinna-rachises up to 2 cm. long. Segments 0.5 cm. long and 0.5 cm. broad to 4 cm. long and 1.0 cm. broad, lanceolate to narrowly oblong, entire or ternately divided, subcoriaceous, the borders whitish, crenulate, mucronate, the mucro 0.5–1.5 mm. long, flat or reflexed, with a whitish margin contiguous with that of the segment. Sporangia long stalked, the annulus amber colored; glands with ceraceous indument may occur among the sporangia. Spores 64 per sporangium, mostly tetrahedral-globose, yellow-tan, with a sparse, scarcely prominent, rugose exospore.

*P. ternifolia* is a critical species for it bears relationships to several others and problems relevant to them. The series from this species through *P. brachyptera* shows greater cohesion than any other in the genus. The entities differ by quantitative characters and their ranges for the most part are geographically distinct. The pinnae of *P. ternifolia* var. *Wrightiana* are longer and more dissected than those of *P. ternifolia* var. *ternifolia* and are further expanded in the following two species.

Two chromosome numbers have been reported for *P. ternifolia* var. *ternifolia* by Dr. Britton. A collection from Cuernavaca, State of Morelos in Mexico, R. M. & A. F. Tryon 5105, and one from El Pedregal on the south edge of Mexico City, R. M. & A. F. Tryon 5146, have chromosome numbers of  $n = 29$ . A collection from Valle de Bravo, State of Mexico, was reported as  $n = 58$  and another from Cuernavaca was a probable polyploid although the number was not definitely established. It is unfortunate that both of the polyploid numbered collections have been lost.

*P. ternifolia* is also suspected of entering into crosses which have produced *P. atropurpurea* and possibly *P. Pringlei*. The range of *P. ternifolia*, though more extensive, resembles that of *P. ovata* but there is no evidence from spore counts, as exists in the latter, of a wide-ranging apogamous strain.

## KEY TO VARIETIES

Blade linear, pinnate or pinnate-pinnatifid; pinnae ternate or entire, without pinna-rachises; southern Texas and Arizona southward along the Cordillera to central Chile, Dominican Republic, Hawaiian Islands.

4A. var. *ternifolia*, p. 150

Blade linear to usually narrowly triangular, bipinnate; pinnae lobed or divided into 3–11 segments, pinna-rachises 4–20 mm. long; southern Oklahoma to northern Mexico. 4B. var. *Wrightiana*, p. 153

4A. *Pellaea ternifolia* var. *ternifolia*.

Fig. 4A. Map 4A.

*Pteris ternifolia* Cav. Descr. Pl. 266. 1802. (Lectotype by C. Christensen in Dansk Bot. Ark. 9:22. 1937: Née, Peru MA; Isotype: F!).

*Pteris peruviana* Poir. in Lam. Ency. Meth. Bot. 5:718. 1804. (Holotype: Joseph Jussieu, Peru P!; Photo: GH!).

*Pteris subverticillata* Sw. Syn. Fil. 103. 1806, based on *Pteris ternifolia* Cav.

*Pteris triphylla* Bertero, in Merc. Chil. 16:748. 1829, nom. nud.; ex Colla, Herb. Pedem. 6:199. 1836. (Holotype: Bertero, in 1828, TO; Isotypes: GH! SGO). Reference as to the type from Looser, in Rev. Univ. (Univ. Cat. Chile) 25:111. 1940; as to the Colla reference, Pichi-Sermoli, in Webbia 8:135. 1951.

*Allosorus subverticillatus* (Sw.) Presl, Tent. Pterid. 153. 1836.

*Platyloma ternifolia* (Cav.) J. Sm. in Bot. Mag. 72: Comp. 21. 1846.

*Allosorus ternifolius* (Cav.) Kze. ex Kl. in Linnaea 20:339. 1847.

*Pellaea Weddelliana* Fée, in Mém. Soc. Mus. Hist. Nat. Strasb. 5:74. 1857. (Mém. Fam. Foug. 8). (Lectotype: Weddell 3778 K!, Isotypes: PI YU!).

*Pellaea lanuginosa* Fée, in Mém. Soc. Hist. Nat. Strasb. 5:114. 1857. (Mém. Fam. Foug. 8) nom. provis. (Holotype: Schaffner 321 P).

*Pellaea mucronata* Fée, Cat. Meth. Foug. Lycop. Mex. 8. 1857. (Mém. Fam. Foug. 9) nom. nud., not (D. C. Eaton) D. C. Eaton, in Torr. U. S. & Mex. Bound. Bot. 233. 1859. (Isotype: Schaffner 150 YU!).

*Cbeilanthes lanuginosa* (Fée) Moore, Ind. Fil. 255. 1861; not Mett. ex Hook. Syn. Fil. 2:99. 1858, nor Mart. & Gal. in Mém. Acad. Brux. 15:75. 1842.

*Cbeilanthes Weddelliana* (Fée) Moore, Ind. Fil. 255. 1861.

*Cbeilanthes ternifolia* (Cav.) Moore, loc. cit.

*Notbochlaena ternifolia* (Cav.) Keyserl. Polyp. Cyath. Herb. Bung. 29. 1873.

*Adianthus ternatum* Sessé & Moc. Pl. Nov. Hisp. 182. 1887–90; ed. 2. 169. 1893, not Humb. & Bonpl. ex Willd. 1810.

*Pellaea ternifolia* var. *petiolulata* C. Chr. in Ark. Bot. 20: 18. 1926. (Holotype: Asplund 3071 UPS, Isotype: US!).

*Cassebeera ternifolia* (Cav.) Farw. in Amer. Midl. Nat. 12:281. 1931.

*Pellaea Brandegeei* C. C. Hall, in Amer. Fern Journ. 37:111. 1947. (Holotype: Brandegee, Mexico UC!, Isotype: US!).

Scales of the rhizome and base of the stipes bicolorous with a slender central sclerotic stripe usually narrower than the border, the margins entire at the base, dentate above. Stipe and rachis plane on the upper surface or sulcate, atropurpureous or black. Blade linear to narrowly lanceolate, once pinnate. Pinnae ternate or entire, sessile or subsessile, without pinna-rachises. Without glands among the sporangia.

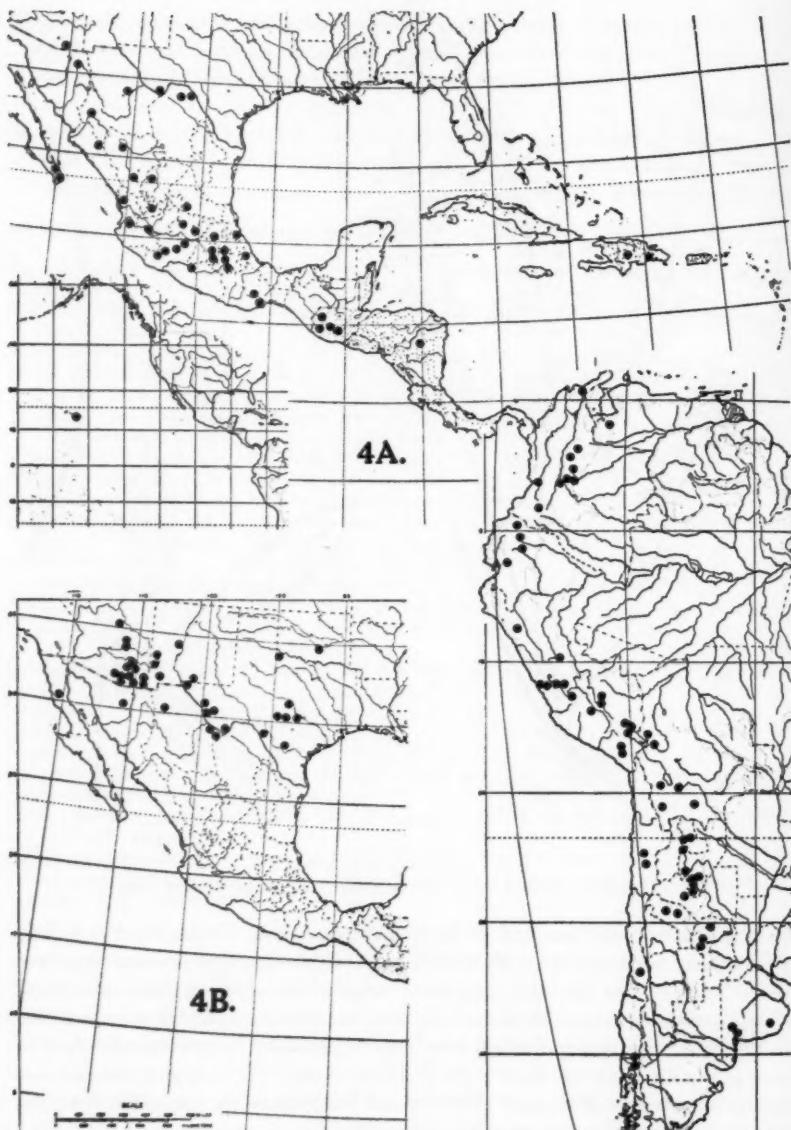
Several segregates of *P. ternifolia* var. *ternifolia* have been made on differences in the form of the pinnae, length of the pinna-rachises and serration and color of the scales. Such variations are not sufficiently clear for taxonomic recognition although they are of interest in the dynamics of the species. The segregates, *P.*



Fig. 4A. *Pellaea ternifolia* var. *ternifolia*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

*Brandegeei* at the southern end of Baja California and *P. Weddelliana* in Bolivia and northern Argentina show slight differences which would be expected in populations isolated from the main geographic range of the species. Collections from several localities in central Mexico which have entire pinnae, pubescent rachises and lax fronds are presumably Fée's *P. lanuginosa*. This may be cytologically distinct for a pubescent specimen from Valle de Bravo is reported to have a chromosome number of  $n = 58$ . Two other collections of *P. ternifolia* var. *ternifolia* from the vicinity of Mexico City are reported as  $n = 29$ .

In crevices or among igneous rocks, on dry earthen walls in Peru, in sun or semi-shade, at 200–4000 m.



4A. Distribution of *Pellaea ternifolia* var. *ternifolia*, 4B. var. *Wrightiana*.

1957]

Southern Arizona and Texas; Mexico; Guatemala; Nicaragua; Hispaniola; Venezuela, Colombia to Argentina; Hawaiian Islands.

Representative specimens:

UNITED STATES. ARIZONA: Phillips et al. 2565 (US). TEXAS: E. J. Palmer 34165 (GH, MO, NY); R. M. & A. F. Tryon 5097 (GH, K, MO, MEXU, U, UC, US, UT).

MEXICO. BAJA CALIFORNIA: Jones 27013 (MO, NY, UC, US); Cape Region, in 1893, Brandegee (UC). CHIHUAHUA: Pringle 920 (F, GH, MO, US); E. Palmer 452 (GH, MO, NY, US, YU). COAHUILA: Wynd & Mueller 574 (GH, MO, NY, US). DURANGO: Pennell 18258 (F). GUANAJUATO: Sept. 1900, Dugés (GH). GUERRERO: Hinton 10490 (F, MO, NY, US). HIDALGO: Clokey 1892 (MO). JALISCO: McVaugh 12998 (US); E. Palmer 764 (US, YU). MEXICO: Lyonnet 26 (GH, MO, NY, US); Matuda 26023 (US); R. M. & A. F. Tryon 5137, 5141 (MEXU, MO), 5146 (MEXU, MO, US). MICHOACÁN: Arsène 1975 (US). MORELOS: Orcutt 3827 (GH, MO, US); R. M. & A. F. Tryon 5102 (MEXU, MO). OAXACA: Conzatti 1401 (GH). PUEBLA: Arsène 1995 (GH, MO, US). QUERÉTARO: Arsène 10654 (US). SAN LUIS POTOSÍ: Parry & Palmer 982 (F, MO, NY, US, YU). SINALOA: Gentry 6434 (MO). SONORA: White 4221 (GH). TLAXCALA: Hernández-Kolocotz 334 (US); Sharp & Hernández 44445 (US). VERACRUZ: Seaton 279 (F, GH, US). ZACATECAS: Rose 2792 (US).

GUATEMALA: Skutch 806 (GH, UC); Standley 58350 (F, US).

NICARAGUA: Standley 11005 (F).

DOMINICAN REPUBLIC: Ekman 11706 (NY, US); R. H. & E. S. Howard 9137 (GH, MO, NY, US).

VENEZUELA. MÉRIDA: Gebriger 251 (US).

COLOMBIA. BOYACÁ: Fosberg 22210 (US). CUNDINAMARCA: Pennell 2548 (F, GH, MO, NY, US). VALLE: Cuatrecasas 20829 (F, US). CAUCA: Killip 6882 (GH, NY, US). MAGDALENA: Seifriz 471 (US). NORTE DE SANTANDER: Garganta 1225 (F). SANTANDER: Killip & Smith 18751 (F, GH, NY, US).

ECUADOR. AZUAY: Rose et al. 22872 (NY, US). IMBABURA: Mexia 7403 (UC, US). LOJA: Fosberg & Giler 23112 (US). PICHINCHA: Heilborn 177 (GH, US). TUNGURA-HUA: Pachano 114 (US).

PERU. Near Guamantanga, Guarimaya Valley, Né (F). AREQUIPA: Pennell 13075 (F, GH, NY, US). CUZCO: Herrera 3172 (F). JUNÍN: Killip & Smith 21817 (NY, US). LA LIBERTAD: Stork & Horton 9997 (F, UC). LIMA: Macbride & Featherstone 286 (F, US). PUNO: R. S. Williams 2633 (GH, NY, US).

BOLIVIA. CHUQUISACA: Tomina, 1845-46, Weddell 3778 (K, P, YU). ORURA: Buchten 1139 (US). POTOSÍ: Asplund 3071 (UPS, US), 4841 (US). LA PAZ: Bang 91 (GH, MO, NY, UC, US); Rusby 323 (GH, US). TARIJA: Fiebrig 3138 (GH, P, UC, US).

ARGENTINA. BUENOS AIRES: Eyerdam et al. 23403 (GH, UC). CATAMARCA: Jörgensen 1251 (GH, MO, UC, US). CORDÓBA: Hieronymus 475 (NY, US). JUJUY: Schulz 972 (GH); West 6249 (US). LA RIOJA: Hunziker 5278 (MO). SALTA: Venturi 9983 (GH). TUCUMÁN: Venturi 10428 (GH, MO).

CHILE. ANTOFAGASTA: Johnston 5305 (GH, US). CAUTÍN: Claude-Joseph 2658 (US). O'HIGGINS: May 1828, Bertero (GH). VALDIVIA: Hollermayer 1898 (MO, US).

HAWAIIAN ISLANDS. HAWAII: Mann & Brigham 262 (GH, MO, US). MAUI: Degener & Wiebke 3975 (GH, MO, US). OAHU: Degener 10419 (MO, US).

4B. *PELLAEA TERNIFOLIA* var. *Wrightiana* (Hook.) A. F. Tryon, comb nov.

Fig. 4B. Map 4B.

*Pellaea Wrightiana* Hook. Sp. Fil. 2:142. 1858. (Holotype: Wright 2130 K!, Isotypes: GH! NY! US! YU!).

*Cibilanthes mucronata* var. *Wrightiana* (Hook.) Moore, Ind. Fil. 248. 1861.

Scales of the rhizome and base of the stipes bicolorous, the central sclerotic stripe as broad or broader than the border, the margins dentate to the base. Stipe

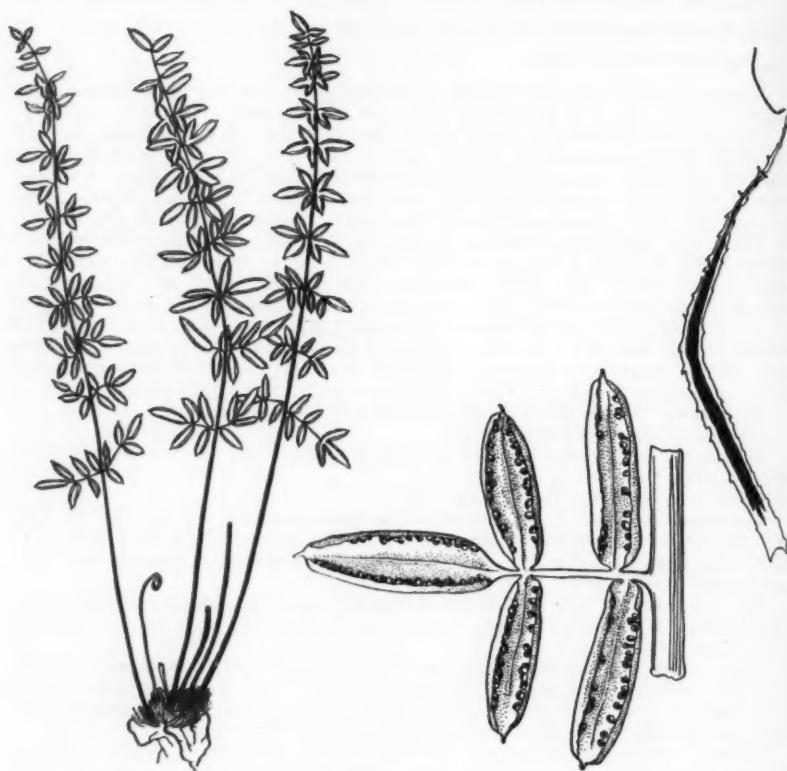


Fig. 4B. *Pellaea ternifolia* var. *Wrightiana*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

and rachis sulcate, castaneous, becoming darker with age. Blade narrowly triangular, bipinnate. Pinnae lobed or divided into 3–11 segments, usually stalked, the pinna-rachises 0.4–2.0 cm. long. Glands with ceraceous indument rarely occur among the sporangia.

*P. ternifolia* var. *Wrightiana* has formerly been treated as a distinct species. It is essentially similar to *P. ternifolia* var. *ternifolia* in the architecture of the blade and is considered a northern extension of the species having quantitative differences not sufficient for specific separation.

In crevices of igneous or limestone rocks or on rocky or gravelly hillsides, full sun or partial shade, at 1400–2300 m.

Oklahoma to Arizona; northern Mexico.

Representative specimens:

UNITED STATES. OKLAHOMA: Waterfall 6456 (GH). TEXAS: Moore & Steyermark 3019 (GH, MO, NY, US); Mueller 8265 (GH, MO, US); E. J. Palmer 34260 (F, MO, NY); Reverchon 1216 (F, GH, MO, NY, US); R. M. & A. F. Tryon 5041 (MO, US) 5096 (GH, K, MO, U, US). NEW MEXICO: Eastwood 8266 (GH, US); Gooddng 766 (GH, NY, US); Dec. 1880, Rusby (MO, US, YU); 1851, Wright 2130 (GH, K, NY, US, YU). ARIZONA: Blumer 1867 (F, NY, US); Sept. 1880, Engelmann (MO); B. & R. R. Maguire 12027 (US); Phillips & Reynolds 2943 (GH, US).

MEXICO. BAJA CALIFORNIA: April 1889, Brandegee (GH, US); Gentry 4283 (GH, MO). CHIHUAHUA: Johnston 8090 (GH); Pennell 19209 (US). COAHUILA: Johnston & Muller 1309 (GH). SONORA: 1895, Druery (US).

5. *Pellaea longimucronata* Hook. Sp. Fil. 2:143. 1858. (Holotype: Wright 2131 K!, Photo: GH!, Isotypes: GH! US! YU!). Fig. 5. Map 5

*Pellaea Wrightiana* var. *longimucronata* (Hook.) Davenp. Cat. Davenp. Herb. Suppl. 46. 1883.

*Pellaea truncata* Gooddng, in Muhlenb. 8:94. 1912. (Holotype: Gooddng 977 US!). *Cassebeera ternifolia* var. *longimucronata* (Hook.) Farw. in Amer. Midl. Nat. 12:282. 1931.

Rhizome moderately stout, elongate, decumbent, multicapitular. Scales of the rhizome and base of the stipes appressed, brown, bicolorous, with a central sclerotic stripe usually broader than the border, subulate, straight or falcate, the margin erose-dentate, the cells of the border trapezoidal, usually not more than five times longer than broad, the apex dentate, not attenuate. Fronds 12–38 cm. long, erect, straight and stiff, monomorphic, the lower pinnae often sterile, the upper fertile, the buds sparsely pubescent. Stipe and rachis sulcate, glabrous or nearly so, usually glaucous, castaneous becoming darker with age, the stipe breaking irregularly without articulation lines, the rachis of the mature frond castaneous to the terminal pinna. Blade 8 cm. long and 4 cm. broad to 22 cm. long and 12 cm. broad, triangular, acuminate, bipinnate, rarely tripinnate, grayish green, the lower pinnae longer, departing at broad angles to the rachis, once pinnate with 9–21 segments, rarely bipinnate, sessile or short stalked, the pinna-stalks not decurrent, the axes colored as the rachis, the pinna-rachises up to 7 cm. long. Segments 0.3 cm. long and 0.1 cm. broad to 1.5 cm. long and 1.0 cm. broad, narrowly oblong to oval, entire, subcoriaceous, the border narrow, white, crenulate or dentate, mucronate, the mucro 0.5–2.0 mm. long, flat or reflexed, green at the base, with a white margin extending into the attenuate apex and contiguous with the borders of the segment. Sporangia usually long stalked, the annulus amber colored, glands with ceraceous indument occurring among the sporangia. Spores 64 per sporangium, mostly tetrahedral-globose, yellow-tan, the exospore of short, scarcely prominent rugae.

During field studies made in July and August of 1950 in southern Texas, New Mexico and Arizona six species of the section were collected and *P. longimucronata* was most frequently encountered. It grows in extremely xeric habitats often devoid of other vegetation.

In clefts of igneous rocks or among boulders or gravelly soil, in open sun, at 1250–2000 m.

Texas to Colorado, Arizona, Utah, Nevada; northern Mexico.



Fig. 5. *Pellaea longimucronata*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

#### Representative specimens:

UNITED STATES. TEXAS: Correll 13799 (MO), 15049 (MO); Hinckley 2585 (GH, NY, US); R. M. & A. F. Tryon 5086 (GH, MO, US); Waterfall 4568 (GH, MO). COLORADO: April 24, 1874, Brandegee (F, MO); Sept. 25, 1874, Engelmann (MO). NEW MEXICO: Sept. 10, 1880, Rusby (F, GH, MO, NY, US, YU); R. M. & A. F. Tryon 5087 (GH, K, MEXU, MO, U, US); 1897, Wootton 99 (MO, NY, US); 1851-52, Wright 2131 (GH, K, NY, US). UTAH: Gould 1740 (NY, US); Palmer 497 (NY). ARIZONA: Blumer 1970 (GH, US); Mule Mts., Aug. 1911, Goedding 977 (US); Palmer 649 (F, MO, YU); March 11, 1884, Pringle (F, US); Rotrock 464 (F, GH, MO); R. M. & A. F. Tryon 5099 (MO). NEVADA: Clokey 8257 (F, MO, NY); Goedding 737 (F, GH, MO, NY, US); Jones 5055 (MO, NY).

MEXICO. BAJA CALIFORNIA: April 20, 1889, Brandegee (GH, NY); Palmer 554 (GH). SONORA: E. A. Phillips 511 (GH).

6. *PELLAEA MUCRONATA* (D.C. Eaton) D. C. Eaton, in Torr. U. S. & Mex. Bound. Bot. 233. 1859, not Fée, Cat. Meth. Foug. Lycop. Mex. 8. 1857 (Mém. Fam. Foug. 9) nom. nud.

Rhizome moderately stout, compact or somewhat elongate, decumbent, multi-pinnate. Scales of the rhizome and base of the stipes appressed, brown, bicolorous with a central sclerotic stripe as broad or broader than the border, straight or falcate, subulate, sparsely dentate to entire at the base, dentate to erose above, the cells of the border with oblique end walls, usually not more than five times longer than broad, the apex filiform, tortuous, entangled. Fronds 6.5–43.0 cm. long, erect, stiff, monomorphic, the lower pinnae sometimes sterile, the upper fertile, the buds strongly pubescent or lanate. Stipe and rachis sulcate or plane on the upper surface, glabrous or nearly so, glaucous, castaneous, the stipe often bent or curled, breaking irregularly without articulation lines, the rachis of the mature frond castaneous to the terminal pinna. Blade 3.5 cm. long and 1.0 cm. broad to 25 cm. long and 18 cm. broad, ovate-triangular to rhomboid, acuminate, often abruptly so, bi-to tripinnate, rarely quadripinnate, grayish green, the central or lower pinnae longest, departing at broad or acute angles to the rachis, once pinnate or bipinnate with few to 40 segments, subsessile or short stalked, the pinna-stalks not decurrent, the axils colored as the rachis, the pinna-rachises up to 10 cm. long, exceeding the length of the segments several times. Segments 0.2 cm. long and 0.1 cm. broad to 1.2 cm. long and 0.6 cm. broad, narrowly oblong, entire or ternate, subcoriaceous, the border undifferentiated, crenate, mucronate, the mucro 0.25–1.50 mm. long, flat, thickened, green at the base, the apex lutescent, distinct from the revolute borders of the segment. Sporangia short stalked, the annulus amber colored, glands with ceraceous indument occurring among the sporangia. Spores 64 per sporangium, mostly tetrahedral-globose, yellow-tan, with a sparse, scarcely prominent rugose exospore.

#### KEY TO VARIETIES

- Pinnae distant, not imbricate, at broad angles to the rachis; pinnules few to 40 per pinna, usually ternate; northern California to Baja California and coastal islands, usually below 1800 m. .... 6A. var. *mucronata*, p. 158
- Pinnae imbricate, especially on the apical portion of the frond, ascending at acute angles to the rachis; pinnules fewer than 20 per pinna, usually entire; Sierra Nevada and southern California, usually above 1800 m. .... 6B. var. *californica*, p. 161

This Californian species exhibits a plasticity of form as great as that of the wider ranging *P. ternifolia*. It occurs among igneous rocks in arid or semi-arid montane regions of the state and is undoubtedly influenced by the topographic and climatic diversities. Mason's<sup>26</sup> observations, especially pertaining to this region,

<sup>26</sup> Madroño 8:209, 241. 1946.

on the effect of topography and climate on the distribution of restricted species helps to interpret the variations of this fern. In southern California Ewan<sup>27</sup> has studied *P. mucronata*, particularly those plants occurring at the higher altitudes. He considers *P. mucronata* var. *californica* to be derived from *P. mucronata* var. *mucronata* through isolation and consequent morphological changes in extreme environments. Less distinct variations in collections of var. *mucronata* from Kern, Tulare and Fresno counties have small, closely set pinnules and have been noted by Maxon.<sup>28</sup> Other specimens from northern California are distinctive in having compound pinnules with 3–11 segments. A few specimens, two of which are cited in the treatment of the next species, have entire pinnules and lax pinnae intermediate between *P. mucronata* var. *mucronata* and *P. brachyptera* and are possibly hybrids.

#### 6A. *PELLAEA MUCRONATA* var. *mucronata*

Fig. 6A. Map 6A.

*Allosorus mucronatus* D. C. Eaton, in Amer. Journ. Sci. 22:138. 1856. (Holotype: Major A. B. Eaton, near Bay of San Francisco, Calif. YU!, Photo: GH!).

*Pelleae longimucronata* var. *minor* Hook. Sp. Fil. 2:143. 1858, nom. nud. based on *Major* A. B. Eaton, Bernica, Calif. K, Isotype: GH!.

*Pellaea ornithopus* Hook. Sp. Fil. 2:143. 1858. (Holotype: Hartweg 2042 K!, Photo: GH!, Isotypes: GH! P!).

*Cheilanthes mucronata* (D.C. Eaton) Moore, Ind. Fil. 45, 248. 1861.

*Allosorus ornithopus* (Hook.) O. Ktze. Rev. Gen. Pl. 2:806. 1891.

*Cassebeera ternifolia* var. *ornithopus* (Hook.) Farw. in Amer. Midl. Nat. 12:282. 1931.

*Cassebeera ternifolia* var. *mucronata* (D.C. Eaton) Farw. loc. cit. 1931.

*Cassebeera ternifolia* var. *stipitata* Farw. loc. cit. (Holotype: Blaisdell, in 1881, MICH!).

Fronds 6.5–43.0 cm. long. Blade 3.5 cm. long and 1.0 cm. broad to 25 cm. long and 18 cm. broad, ovate to rhomboid, bi- or tripinnate, rarely quadripinnate, more or less plane, the apex abrupt or acuminate. Pinnae linear to ovate, not imbricate, at wide angles to and widely spaced on the rachis, those of the mid-region often longer than the basal, with few to 40 segments per pinna. Segments widely spaced on the pinna-rachises, usually ternate.

A collection of Ezra C. Knopf from Santa Catalina Island bears the accompanying information —

"An infusion of the dried leaves of this plant is much prized by the Spanish, Mexicans and some of the white residents, as a tea. I have drunk it and found it quite palatable. It is said to be good for the kidneys and as a blood purifier. After the rainy season is past the plant dries and can be picked any time during the summer. The Indian name is Calagula."

In crevices of igneous rocks or among boulders, full sun or semishade, at 20–2000 m.

California; Baja California.

Representative specimens:

UNITED STATES. CALIFORNIA: Alexander & Kellogg 1993 (MO); Austin 221 (MO, US); Baker 2613 (GH, MO, US); San Diego, 1881, Blaisdell (MICH); H. E. Brown 268 (F, MO, US); Clokey 4840 (MO, P); Bay of San Francisco, Major A. B. Eaton (YU); Oct. 1880, Engelmann (MO); Fosberg R84 (F, MO, US); Hansen 657 (MO, NY, P); Hartweg 2042 (GH, K, P); Heller 7816 (GH, MO, NY, P, US); Kellogg & Harford

<sup>27</sup> Journ. Wash. Acad. Sci. 25:363–370. 1935.

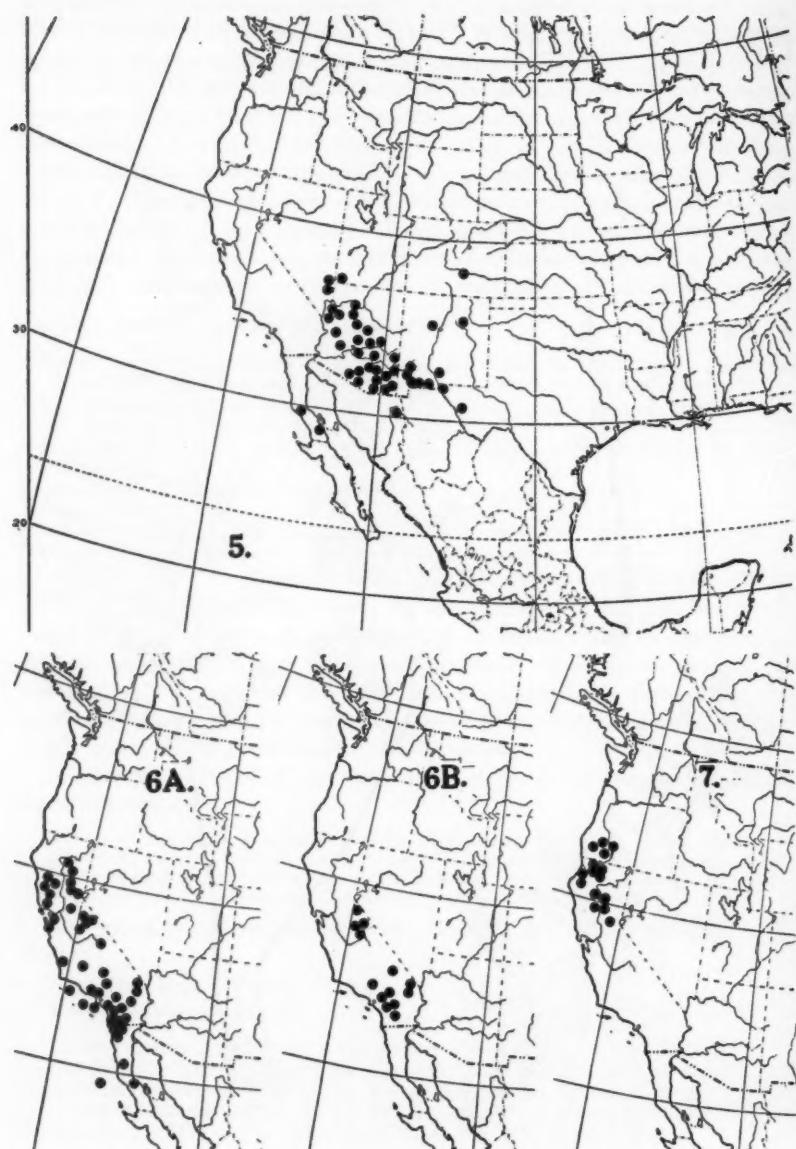
<sup>28</sup> Proc. Biol. Soc. Wash. 30:179. 1917.

1170 (MO, US, YU); McKelvey 5053 (GH, US); Palmer 424 (GH, MO); July 14, 1882, Pringle (GH, MO, US); Torrey 595 (GH, NY, US); R. M. & A. F. Tryon 5058 (GH, K, MEXU, MO, U, UC, US, UT).

MEXICO. BAJA CALIFORNIA: Wiggins 9821 (US); Wiggins & Gillespie 4151 (GH, MEXU, MO, US). GUADALUPE ISLAND: Palmer 100 (GH, MO, NY YU).



Fig. 6A. *Pellaea mucronata* var. *mucronata*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.



5. Distribution of *Pellaea longimucronata*, 6A. Distribution of *Pellaea mucronata* var. *mucronata*, 6B. var. *californica*, 7. Distribution of *Pellaea brachyptera*.

6B. *Pellaea mucronata* var. *californica* (Lemmon) Munz & Johnston, in Amer. Fern Journ. 12:106. 1922.

Fig. 6B. Map 6B.

*Pellaea Wrightiana* var. *californica* Lemmon, Ferns Pacific Coast, 10. 1882. (Lectotype: Lemmon, May 30, 1876, UC!, Isotypes: F! GH! US!).

*Platyloma bella* Moore, in Gard. Chron. 213. 1873. (Holotype: Hort. Veitch. Chelsea, from California K!, Photo: GH!).

*Pellaea bella* (Moore) Baker, Syn. Fil. 477. 1874.

*Pellaea Wrightiana* var. *compacta* Davenp. Cat. Davenp. Herb. Suppl. 46. 1883. (Holo-type: W. G. Wright in 1879, GH!).

*Allosorus bellus* (Moore) O. Ktze. Rev. Gen. Pl. 2:806. 1891.

*Pellaea compacta* (Davenp.) Maxon, in Proc. Biol. Soc. Wash. 30:183. 1917.

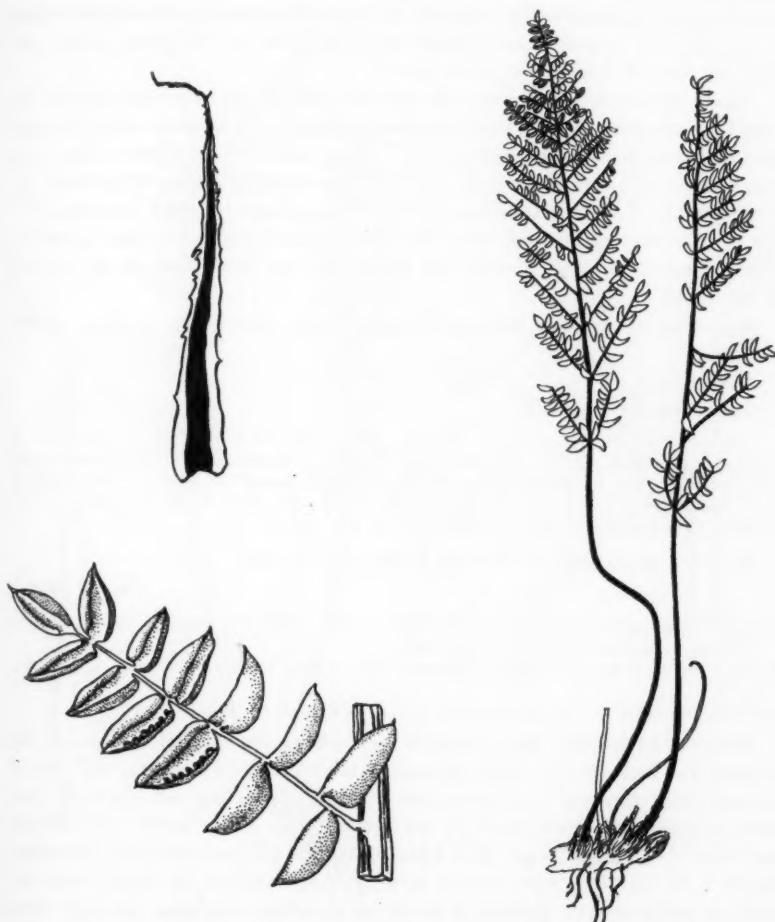


Fig. 6B. *Pellaea mucronata* var. *californica*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

Fronds 9–33 cm. long. Blade 5.5 cm. long and 2.0 cm. broad to 18 cm. long and 8 cm. broad, narrowly deltoid, bipinnate, often conduplicate, acuminate. Pinnae linear, imbricate, usually closely appressed and at acute angles to the rachis, those of the mid-region as long as the basal, with few to 20 segments per pinna. Segments closely placed on pinna-rachises, usually entire.

Some of the earliest collections of this variety from the San Bernardino mountains were made by W. G. Wright. Specimens which he sent to Eaton and Gray are accompanied by letters remarking on the characteristics of the plants which distinguish them from *P. mucronata* var. *mucronata*. His allusion to the pinnae standing back together much as the wings of a bird is a striking one and the character is often apparent in herbarium specimens. The stipe may be curled or bent at the base and proportionately longer than the blade for the plants often grow from the base of boulders or among rocks.

In the absence of a specimen with sufficient data to unquestionably indicate the type I am choosing the above-cited Lemmon specimen. This sheet from the Lemmon Herbarium, collected prior to 1882, is not labeled var. *californica* but bears two tickets—one with locality data and the other labeled "Pellaea Wrightiana var. *compacta* Dav." in Lemmon's handwriting. He apparently added the name after 1883. A collection of 1888 from the same locality, which has been named by Lemmon var. *californica*, matches the earlier one and would indicate his concept of the variety.

On talus, among loose rocks or in rocky woods, open sun or shade, at 1800–3000 m.

California.

Representative specimens:

UNITED STATES. CALIFORNIA: *Abrams* 2084 (GH, MO, NY, US); *Alexander* & *Kellogg* 2948 (UC); *Dudley* & *Lamb* 4648 (F, UC); *Ewan* 9828 (US); *Hoover* 1563 (UC, US); Mt. San Bernardino, May 30, 1876, *J. G. Lemmon* (F, GH, UC, US) B. S. & W. F. *Parish* 511 (F, GH, US); R. M. & A. F. *Tryon* 5061 (GH, K, MEXU, MO, U, UC, US, UT); San Bernardino Mts., 1879, *W. G. Wright* (GH).

#### 7. *Pellaea brachyptera* (Moore) Baker, Syn. Fil. 477. 1874

Fig. 7. Map 7

*Platyloma brachyptera* Moore, in Gard. Chron. 141. 1873. (Holotype: Hort. Veitch. Chelsea, from Calif. K!, Photo: GH! US!).

*Pellaea ornithopus* var. *brachyptera* (Hook.) D.C. Eaton, in Bull. Torr. Bot. Club 4:11. 1873.

*Allosorus brachypterus* (Moore) O. Ktze. Rev. Gen. Pl. 2:806. 1891.

Rhizome moderately stout, elongate, decumbent, multicapitellate. Scales of the rhizome and base of the stipes appressed, ruddy brown, bicolorous, the central sclerotic stripe narrower than the border, often not extending into the scale apex, linear, straight or tortuous, strongly dentate, the cells of the border with oblique end walls, 5–10 times longer than broad, the apex filiform, tortuous, entangled. Fronds 9–39 cm. long, stiff, bent or straight, monomorphic, the buds pubescent. Stipe and rachis sulcate, glabrous or nearly so, glaucous, castaneous, the stipe wiry, often curled, breaking irregularly without articulation lines, the rachis of the

mature frond castaneous to the terminal pinna. Blade 5 cm. long and 1 cm. broad to 20 cm. long and 4 cm. broad, linear, bipinnate, rarely tripinnate, grayish green, the pinnae of nearly the same length, ascending at acute angles and appressed to the rachis, pinnate with 5–13 segments, subsessile or short stalked, the pinna-stalks not decurrent, the axils colored as the rachis, the pinna-rachises up to 2 cm. long, usually shorter than the segments. Segments 0.5 cm. long and 0.2 cm. broad to 2.0 cm. long and 0.4 cm. broad, linear, subcoriaceous, the border strongly revolute, undifferentiated, crenate, mucronate, the mucro 0.25–1.0 mm. long, flat, thickened, green at the base, the apex lutescent, distinct from the revolute borders of the segment. Sporangia short stalked, the annulus amber colored, glands with ceraceous indument occurring among the sporangia. Spores 64 per sporangium,

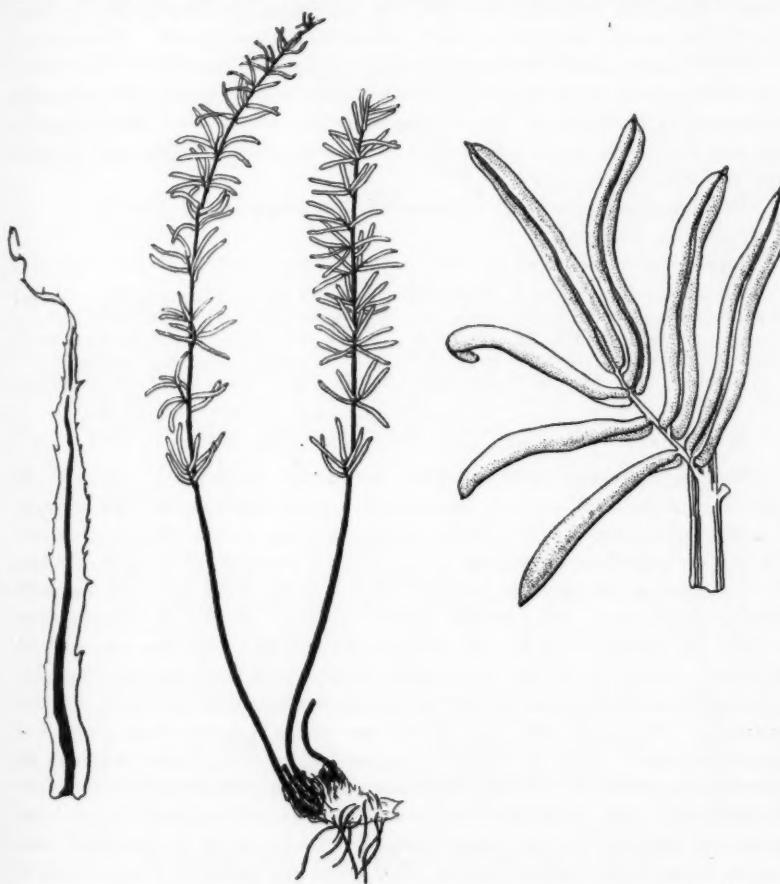


Fig. 7. *Pellaea brachyptera*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

mostly tetrahedral-globose, yellow-tan, with a sparse, scarcely prominent, rugose exospore.

In the search for unusual ferns for English stoves this species was brought from California by Veitch & Sons of Chelsea. The type material grown in the greenhouse in England is more robust than any of the collections from the field. Specimens at the Gray Herbarium and at Yale include some field notes of H. N. Bolander in which he observes that plants from rocks moistened by spray have larger, more numerous segments than those growing among dry rocks. From these observations on the effect of the environment D. C. Eaton concluded that *P. brachyptera* be given only varietal status.

Bolander's collection from the Sierras at 4,000 feet, in 1869 (MO, YU) and that of Kellogg & Harford 1169 (GH, US) are difficult to place as they are intermediate between *P. brachyptera* and *P. mucronata* var. *mucronata*. These two are obviously closely related for their differences are mainly quantitative. The former has shorter pinnae, longer segments, more tortuous rhizome scales as well as a range farther north in California than *P. mucronata* var. *mucronata*. Morphologically the two entities are better defined than in the case of *P. ternifolia* var. *ternifolia* and var. *Wrightiana*.

On talus slopes or basalt or serpentine rock outcrops, at 800-2000 m.  
California, Oregon.

Representative specimens:

UNITED STATES. CALIFORNIA: Constance & Rollins 2933 (GH, MO, US); Copeland 401 (F, GH, MO, NY, P, US); Aug. 1880, Engelmann (MO); July 15, 1907, Heller & Kennedy (F, MO, NY, US); Ownbey & Brown 2424 (GH, MO, NY); Ownbey & Meyer 2198 (MO, NY, US); Wheeler 2744 (GH, MO, NY, US). OREGON: Applegate 2608 (US); July 5, 1887, Howell (F, GH, MO, OSC, US, YU); Thompson 13066 (GH, MO, NY, US).

8. *PELLAEA SAGITTATA* (Cav.) Link, Fil. Sp. Hort. Bot. Berol. 60. 1841.

Rhizome moderately stout, compact, decumbent, multicarpital. Scales of the rhizome appressed and matted, tan to rust colored, concolorous, dull, elongate lanceolate-triangular, usually cordate, straight or nearly so, the margins irregularly dentate, the cells short rectangular or with oblique end-walls or elongate, the apex filiform, more or less tortuous, scales of the base of the stipes and buds appressed, tawny, concolorous, dull, broadly ovate-lanceolate, cordate or pseudopeltate, straight, the margin erose, the cells irregular, sinuous or curved, the apex filiform, tortuous. Fronds 16-78 cm. long, erect, straight, stiff, approximate, dimorphic, the sterile frond shorter and usually with larger segments than the fertile, the buds paleaceous. Stipe and rachis convex or plane on the upper surface, glabrous or puberulous, straw colored to ruddy tan, or mottled, becoming darker with age, the stipe breaking irregularly without articulation lines, the rachis straight or somewhat flexuous, often green in the juvenile frond. Blade 10.0 cm. long and 5.5 cm. broad to 46 cm. long and 32 cm. broad, elongate ovate-triangular or rhomboid, once pinnate or bipinnate, rarely tripinnate, light green, the pinnae at a broad angle to the rachis or ascending, entire or divided into 3-18 segments, long stalked, the pinna-rachises up to 10 cm. long, usually flexuous. Segments 0.5 cm. long and 0.5



8A. Distribution of *Pellaea sagittata* var. *cordata*, 8B. var. *sagittata*.

cm. broad to 5.5 cm. long and 2.75 cm. broad, rotundate-cordate to oblong-sagittate, entire, herbaceous to subcoriaceous, glabrous or puberulent on the under surface and along the margin of the upper surface, veins evident, the border white or lutescent, crenulate, the apex obtuse. Sporangia with short stalks rarely exceeding one half the capsule length, the annulus occasionally irregular-oblique or with a cluster of cells at the apex of the capsule. Spores 64 or 32 per sporangium, ellipsoidal or tetrahedral-globose, yellow or light brown, the exospore with sparse, prominent rugae.

The varieties of *P. sagittata*—*cordata* and *sagittata*—are appropriately named from the form of the segments but are often confused and the matter is further complicated by mixtures of the two under the same number as in the abundant Pringle collections. In addition to the differences in segment form they can be distinguished on several other characters, most easily seen in living plants, as noted in the discussions of the varieties.

The range of the species is extended from Mexico southward to Bolivia by the apogamous variety. In the highlands of central Mexico both types occur in abundance and appear equally vigorous. The apogamous plants do not appear to have any advantage over the normal type except that they, of course, would not require the moisture necessary for fertilization. The two varieties usually grow a few miles apart in colonies of a few to 25 independent plants but on calcareous soils near Cuernavaca, Mexico, I have found them growing together. Preliminary cytology work indicates that the apogamous var. *sagittata* is a triploid with 87 chromosomes. The collections which have been cytologically examined by Dr. Britton are from Mexico. One near Morelia in the state of Michoacán collected by R. M. & A. F. Tryon 5153 had both n and 2n chromosome numbers of 87. Collections of var. *cordata* 5147 and 5149 from El Pedregal in the Distrito Federal were both reported as probably n = 29 by Dr. Britton. It seems possible that the latter and *P. ovata*, which has both normal and apogamous strains, are the most likely parents of *P. sagittata* var. *sagittata*.

#### KEY TO VARIETIES

- Segments rotundate-cordate; rachis and segment stalks glabrous; spores 64 per sporangium, tetrahedral-globose, 37–53  $\mu$  at broadest diameter; southern Texas southward in Mexico to Oaxaca.....8A. *P. sagittata* var. *cordata*, p. 166  
Segments ovate-triangular to sagittate; rachis and segment stalks usually puberulous; spores 32 per sporangium, ellipsoidal, 53–106  $\mu$  at broadest diameter; Chihuahua, Mexico, southward to Bolivia.....  
.....8B. *P. sagittata* var. *sagittata*, p. 168

8A. *PELLAEA SAGITTATA* var. *cordata* (Cav.) comb. nov. Fig 8A. Map 8A.

*Pteris cordata* Cav. Descr. Pl. 267. 1802. (Holotype: Née, Chapultepec, Mexico MA, Isotype: Fl!).

*Allotorus cordatus* (Cav.) Presl, Tent. Pterid. 153. 1836.

*Platyloma cordata* (Cav.) J. Sm. in Journ. Bot. ed. W. J. Hooker 4:160. 1841.

*Pellaea cordata* (Cav.) J. Sm. Cat. Kew Ferns, 4. 1856, not Féé, 1850–52.

*Nothochlaena cordata* (Cav.) Keyserl. Polyp. Cyath. Herb. Bung. 29. 1873.  
*Adiantum cordifolium* Sessé & Moc. Pl. Nov. Hisp. 182. 1887–90; ed. 2, 169. 1893.  
*Cassebeera cordata* (Cav.) Farw. in Amer. Midl. Nat. 12:281. 1931.  
*Pellaea cardiomorpha* Weather. in Journ. Arn. Arb. 24:309. 1943, based on *Pteris cordata* Cav.

Rachis and segment stalks glabrous. Blade rather lax in habit, the pinnae at broad angles to the rachis. Segments 0.5 cm. long and 0.5 cm. broad to 3.0 cm. long and 2.75 cm. broad, rotundate-cordate. Spores 35–53  $\mu$  at greatest diameter, 64 per sporangium, mostly tetrahedral-globose with trilete commissural ridges.

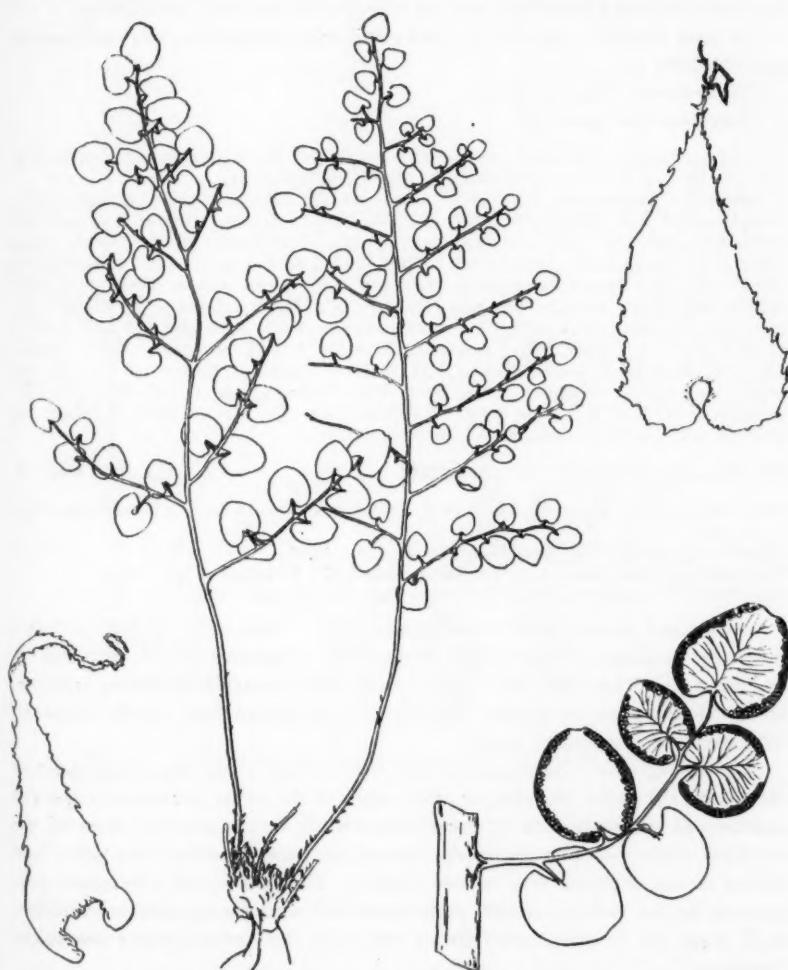


Fig. 8A. *Pellaea sagittata* var. *cordata*, plant  $\times \frac{1}{2}$ ; pinna; left, rhizome scale, right, stipe scale.

Variety *cordata* is distinguished from var. *sagittata* in the lax habit of the fronds, the pinnae at broad angles to the rachis, glabrous stipes and rachises and sporangia with 64 spores, in addition to the cordate form of the segments.

Cavanilles cites Née collections from Chalma and Chapultepec, Mexico, under *Pteris cordata* and the holotype at Madrid is indicated by Christensen<sup>29</sup> as the Chapultepec specimen. Two fragments, one of var. *cordata* and the other of var. *sagittata* from the Née collection, on a single sheet in the Chicago Natural History Museum herbarium are labeled Chalma & Chapultepec. The larger specimen is var. *cordata* from Chapultepec and the other is var. *sagittata* from Chalma.

In open or shade, moist or dry rocks, andesitic, porphyritic, lava or limestone, at 1900–2900 m.

Southwestern Texas to Oaxaca.

Representative specimens:

UNITED STATES. TEXAS: Hinckley 1010 (NY, US); E. J. Palmer 34301 (GH, NY, US); R. M. & A. F. Tryon 5081 (GH, K, MEXU, MO, U, US).

MEXICO. Chapultepec, Née (F). CHIHUAHUA: LeSueur 1139 (UC, GH, US); Pringle 448 (F, GH, MEXU, MO, NY, UC, US, YU). COAHUILA: Wynd & Mueller 590 (GH, MO, NY, US). DISTRITO FEDERAL: Matuda 18828 (US); R. M. & A. F. Tryon 5103 (MO), 5147 (MO), 5149 (GH, MEXU, MO, US). GUANAJUATO: Kenoyer 1787 (US). HIDALGO: Rose & Painter 6741 (GH, NY, US); R. M. & A. F. Tryon 5124 (GH, MEXU, MO, US). MEXICO: Bourgeau 685 (GH, NY, P, US); Lemmon 50 (F, GH, UC, US); Rose & Painter 6825 (GH, US). MICHOACÁN: Arsène 2970 (MEXU, MO, P, US); C. & E. Seler 1233 (GH, US). MORELOS: R. M. & A. F. Tryon 5121 (MO). NUEVO LEÓN: C. H. & M. T. Mueller 970 (F, GH, MEXU). OAXACA: Conzatti & González 521 (GH), 521a (GH). PUEBLA: Arsène 9961 (US); Purpus 2712a (F, GH, NY, UC, US). QUERÉTARO: J. N. & J. S. Rose 11106 (NY, US). SAN LUIS POTOSÍ: Parry & Palmer 980 (F, MO, NY, US, YU). ZACATECAS: Lloyd 247 (US).

#### 8B. *Pellaea sagittata* var. *sagittata*.

#### Fig. 8B. Map 8B.

*Pteris sagittata* Cav. Descr. Pl. 267. 1802. (Holotype: Née, Cerro de Guadeloupe, Mexico MA).

*Allosorus sagittatus* (Cav.) Presl, Tent. Pterid. 153. 1836.

*Platyloma sagittata* (Cav.) J. Sm. in Journ. Bot. ed. W. J. Hooker 4:160. 1841.

*Pellaea cordata* f. *sagittata* (Cav.) Davenp. in Bot. Gaz. 21:261. 1896.

Rachis and segment stalks usually puberulous. Blade stiff and erect in habit, the pinnae ascending at acute angles to the rachis. Segments 0.5 cm. long and 0.5 cm. broad to 5.5 cm. long and 2.0 cm. broad, ovate-triangular to oblong-sagittate. Spores 53–106  $\mu$  at the greatest diameter, 32 per sporangium, mostly ellipsoidal with monolete commissural ridge.

Variety *sagittata* is distinguished from var. *cordata* in the erect, rigid habit of the fronds, the pinnae ascending at acute angles to the rachis, puberulous stipes and rachises and sporangia with 32 spores, in addition to the sagittate form of the segments. The tawny scales of the base of the stipes and buds are fewer and smaller in var. *sagittata* than in var. *cordata*. The presence of pubescence, particularly on the rachises, appears to be correlated with the apogamous condition. In *P. ovata* and *P. andromedaeifolia*, as well as in this variety, it is a convenient

<sup>29</sup> Dansk Bot. Ark. 9:23. 1937.

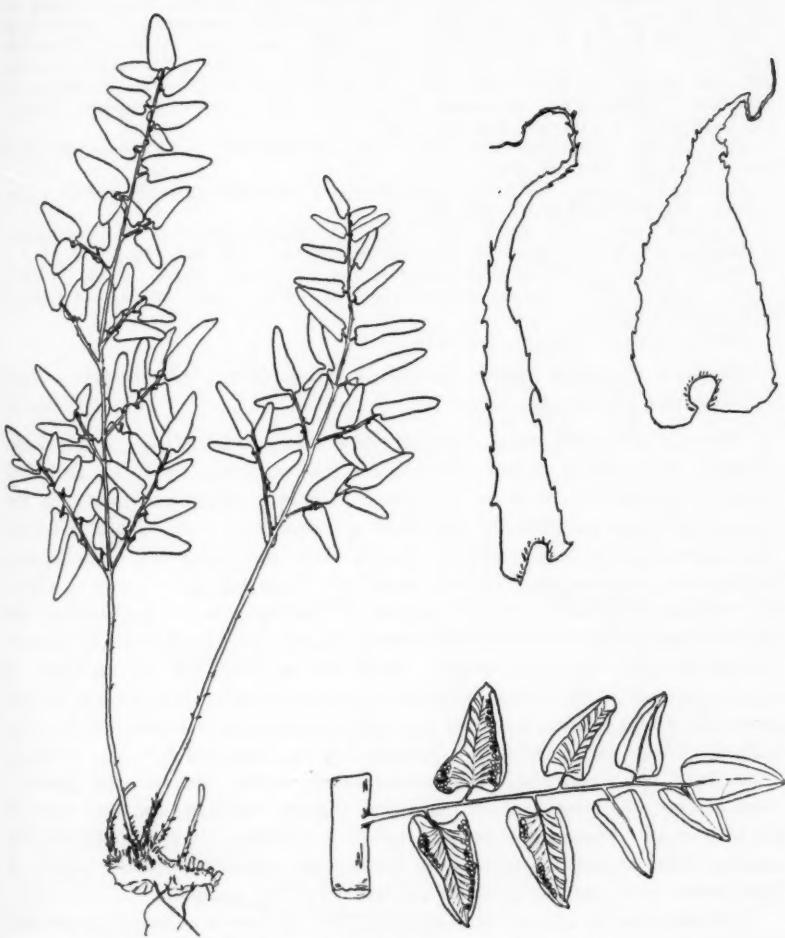


Fig. 8B. *Pellaea sagittata* var. *sagittata*, plant  $\times \frac{1}{2}$ ; pinna; left, rhizome scale, right, stipe scale.

clue for detecting specimens with 32 spored sporangia and apparently apogamous.

On dry banks, in open or shade, among limestone rocks, on adobe walls or stone fences, at 1700–3000 m.

Northern Mexico to Guatemala; Colombia to Bolivia.

Representative specimens:

MEXICO. CHIAPAS: Gbriesbregt 303 (F, GH, YU). CHIHUAHUA: Knoblock 5940 (GH, MSC, US). DISTRITO FEDERAL: Matuda 26234 (US). HIDALGO: Mexia 2760 (UC).

JALISCO: *McVaugh 12974* (US). MEXICO: *Bourgeau 1163* (GH, P); *Rose et al. 9464* (F, US); *R. M. & A. F. Tryon 5138* (GH, MEXU, MO, US). MICHOACÁN: *Arsène 6546* (MEXU, MO, US); *R. M. & A. F. Tryon 5153* (MO). MORELOS: *Hitchcock & Stanford 7089* (UC); *R. M. & A. F. Tryon 5122* (MEXU, MO). OAXACA: *Conzatti & González 428* (GH, MEXU, P); *Pringle 4887* (GH, MEXU, MO, NY, P, UC, US). PUEBLA: *Arsène 7027* (GH, MO, US). TLAXCALA: *Arsène 9971* (US). SAN LUIS POTOSÍ: *Schaffner 959* (GH, YU). ZACATECAS: *Rose 2795* (GH, US).

GUATEMALA: QUEZALTENANGO: *Skutch 805* (F, GH, US). SANTA ROSÁ: *Heyde & Lux 6282* (F, GH, MO, NY, US).

COLOMBIA: CAUCA: *Killip 6877* (GH, NY, US); *Lehmann 5710* (F, P, US). SANTANDER: *Killip & Smith 17440* (NY, US).

ECUADOR: IMBABURA: *Mexia 7428* (UC, US); *Wiggins 10272* (US). PICHINCHA: *Asplund 6297* (US); *Coutinho 39* (GH, YU); *Mille 130* (GH, MO, US).

PERU: APURIMAC: *Stork et al. 10648* (F, UC). CUZCO: *Herrera 1195* (F, US); *Vargas 11049* (F, UC). HUANCavelica: *Tovar 317* (US). LIMA: *Macbride & Featherstone 422* (F, GH, US).

BOLIVIA: LA PAZ: *Mandon 1554* (GH).

9. *PELLAEA NOTABILIS* Maxon, in Contrib. U. S. Nat. Herb. 10:500. 1908.  
(Holotype: *Palmer 234* US!). Fig. 9. Map. 9.

Rhizome moderately stout, compact, decumbent, multicarpital. Scales of the rhizome appressed and matted, rust colored, the young tips light tan, these and those at the base of the stipes concolorous, subulate, straight or nearly so, the margins pectinate-serrulate, the cells short rectangular or with oblique end-walls or elongate, the apex long attenuate. Fronds 12–43 cm. long, erect, straight, stiff, approximate, monomorphic, the buds pubescent. Stipe and rachis terete or elliptical, pubescent, the rachis and upper portion of the stipe straw to buff colored, the stipe base and segment stalks atropurpureous, the stipe breaking irregularly without articulation lines, the rachis straight. Blade 3.5 cm. long and 3.5 cm. broad to 23 cm. long and 14 cm. broad, deltoid or elongate-triangular, once pinnate, grayish green, the pinnae at broad angles to the rachis or somewhat ascending, entire, short stalked, without pinnae-rachises. Segments 3.0 cm. long and 0.75 cm. broad to 7 cm. long and 1 cm. broad, elongate-lanceolate, entire, subcoriaceous, glabrous, veins obscure, the border narrow, lutescent, slightly crenulate, the apex more or less mucronate. Sporangia with short stalks not exceeding the capsule length, the annulus amber colored. Spores 64 per sporangium, tetrahedral-globose, yellow or light brown with prominent, rugose and somewhat lacy exospore.

Although clearly unique, the position of this rare fern is intermediate between the dark and light striped groups. It resembles *P. atropurpurea* in having concolorous scales, terete rachises and atropurpureous color at the base of the stipes and petiolules. Similarities to *P. ovata* and *P. sagittata* occur in the predominant straw color of the rachises and stipes, the prominent spore ornamentation and the pectinate-serrulate scales. The subulate form of the scales is similar to *P. ovata* and both of these species have been collected in Tamaulipas. Since there are so few collections of *P. notabilis* I searched for it at some length in the vicinity of Monterrey—but with no success. It appears to be a rare fern possibly restricted to select ecological niches which are explored with some difficulty in that region.

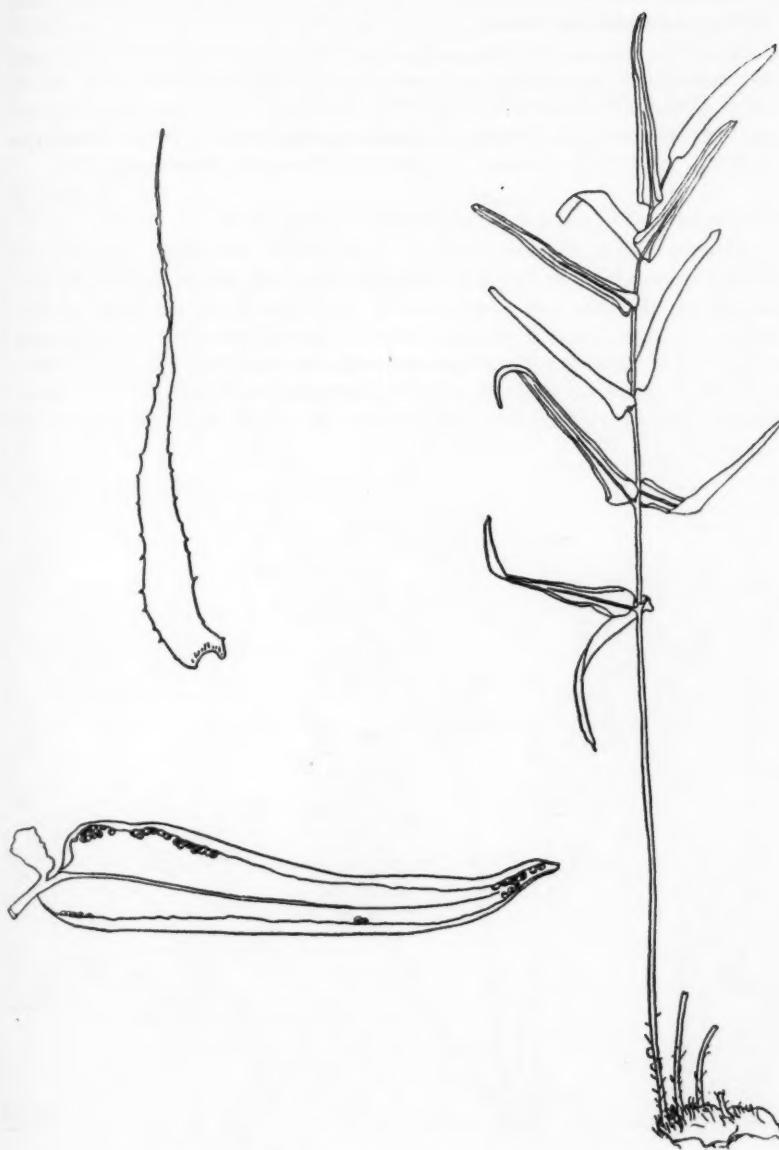


Fig. 9. *Pellaea notabilis*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

Among rocks, at 320–1100 m.

Tamaulipas and Nuevo León.

MEXICO. NUEVO LEÓN: *Sanchez* 316 (US). TAMAULIPAS: *Bartlett* 10352 (US); 1902, *Kemp* (NY); among rocks in cañon, vicinity of Victoria, alt. about 320 m., Feb. 1–April 9, 1907, *E. Palmer* 234 (US); *Stanford et al.* 2129 (US).

10. *Pellaea Pringlei* Davenp. in Gard. & For. 4:555. 1891. (Holotype: *Pringle* 2591 GH!, Isotypes: F! MO! US!, Paratype: *Palmer* 543 US!).

Fig. 10. Map 10.

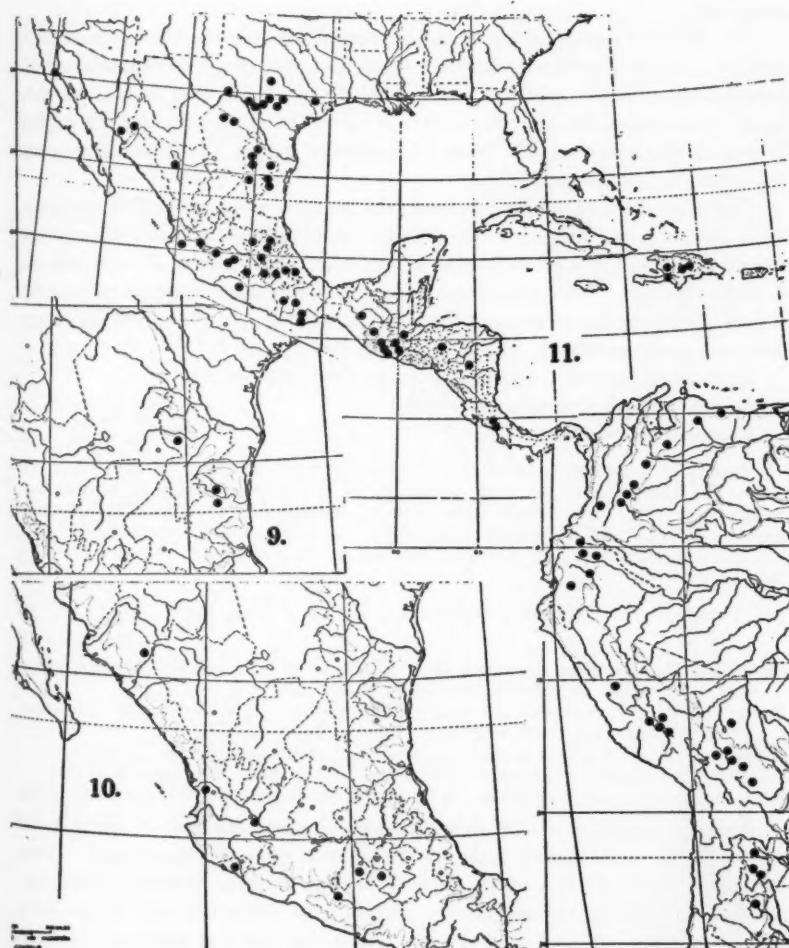
*Allosorus Pringlei* (Davenp.) O. Ktze. Rev. Gen. Pl. 2:806. 1891.

Rhizome moderately stout, compact, multicarpital, decumbent. Scales of the rhizome appressed, tan to ruddy brown, these and those of the base of the stipes concolorous, the scale base often sclerotic and adherent to the stipe, acicular, straight or nearly so, the margins entire or sparsely dentate, the cells short-rectangular or elongate with oblique end-walls, the apex long-attenuate. Fronds 6–47 cm. long, erect, straight or nearly so, approximate, the sterile fronds shorter, the buds covered with subulate scales. Stipe and rachis convex or plane on the



Fig. 10. *Pellaea Pringlei*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

upper surface, or channeled, more or less paleaceous, the rachis and upper portion of the stipe straw-yellow or mottled, the stipe base darker, usually atropurpureous, the stipe breaking irregularly without articulation lines, the rachis straight. Blade 4.0 cm. long and 2.5 cm. broad to 20 cm. long and 13 cm. broad, elongate-triangular, once pinnate or bipinnate, bluish green, the pinnae ascending, entire or with 2-3 segments, usually long stalked, the pinna-rachises less than 0.5 cm.



9. Distribution of *Pellaea notabilis*, 10. Distribution of *Pellaea Pringlei*, 11. Distribution of *Pellaea ovata*.

long, usually absent. Segments 0.75 cm. long and 1.0 cm. broad to 4.0 cm. long and 4.5 cm. broad, deltoid-hastate or stellate, entire, ternate or with 3–5 irregular lobes, chartaceous or herbaceous, glabrous, the veins evident, the border whitish crenulate, often opaque, bluish on the upper surface. Sporangia stalks short, one fourth the capsule length, the annulus amber colored, occasionally irregular-oblique or with a cluster of cells at the apex of the capsule. Spores 64 per sporangium, tetrahedral-globose, yellow or brownish, with prominent rugose-reticulate exospore.

The complete specimens and ample number of collections of these pellaeas made by C. G. Pringle have made possible a better understanding of the group. From his carefully prepared specimens one receives the impression that he admired these ferns. It is appropriate that this attractive species bears his name for the original as well as the most complete suites of specimens are his. It is uncommon and few others have collected it.

The stipes are largely straw colored, the pinnae star-shaped and bluish green. Some specimens are irregularly lobed rather than stellate and have incompletely formed spores. It is possible that the species may be a hybrid of *P. ternifolia* and *P. ovata* although it has distinctive acicular and largely concolorous rhizome scales. It occurs on moist limestone along the banks of streams partially within the ranges, but much more restricted, than those two species.

Uncommon, on wet calcareous banks, at 1000–2200 m.

Sinaloa south to Guerrero and Morelos.

Representative specimens:

MEXICO. COLIMA: Reko 4846 (US). GUERRERO: Hinton 9475 (F, NY, US). JALISCO: Río Blanco, June–Oct. 1886, Palmer 543 (US, YU); Cool mossy banks near Guadalajara, Oct. 19, 1889, Pringle 2591 (F, GH, MEXU, NY, P, US, YU). MEXICO: Hinton 1537 (GH, MEXU), 4227 (GH, NY). MORELOS: Pringle 7949 (F, GH, MO, NY, US); Sanchez 97 (US). NAYARIT: Mexia 709 (US). SINALOA: Gentry 6523 (GH, MO).

#### 11. *PELLAEA OVATA* (Desv.) Weatherby, in Contr. Gray Herb. 114:34. 1936.

Fig. 11. Map 11.

*Pteris ovata* Desv. in Mém. Soc. Linn. Paris (Prodrome de la famille des Fougères) 6:301. 1827. (Holotype: Peru, Herb. Desvaux P!, Photo: GH! UCI!).

*Pteris flexuosa* Kaulf. ex Schlect. & Cham. in Linnaea 5:614. 1830, excl. synon. (Holotype: Schiede & Deppe, Aug. 1828, near Jalapa, Mexico, B).

*Allosorus flexuosus* (Kaulf. ex Schlect. & Cham.) Kze. in Linnaea 13:136. 1839.

*Pellaea flexuosa* (Kaulf. ex Schlect. & Cham.) Link, Fil. Sp. Hort. Bot. Berol. 60. 1841.

*Platyloma flexuosa* (Kaulf. ex Schlect. & Cham.) J. Sm. in Bot. Mag. 72: Comp. 21. 1846.

Rhizome slender, cord-like, dichotomously branched, creeping or compact and enveloped by matted roots. Scales of the rhizome appressed, tan to dark brown, these and those at the base of the stipes bicolorous, elongate, lanceolate-triangular, cordate, the sclerotic central portion lustrous (old scales sclerotic except for a narrow margin), straight or somewhat falcate, the margins pectinate to erose-serrulate, the cells short-rectangular or with oblique end-walls, the apex filiform, more or less tortuous. Fronds 10–125 cm. long, straight or frequently twining,

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subcendent, approximate, monomorphic, the buds on old portions of the rhizome as well as the apex, lanate to pubescent, with a few scales. Stipe and rachis convex or plane on the upper surface, glabrous or pubescent, straw colored to ruddy brown becoming gray with age, the stipe breaking irregularly without articulation lines,

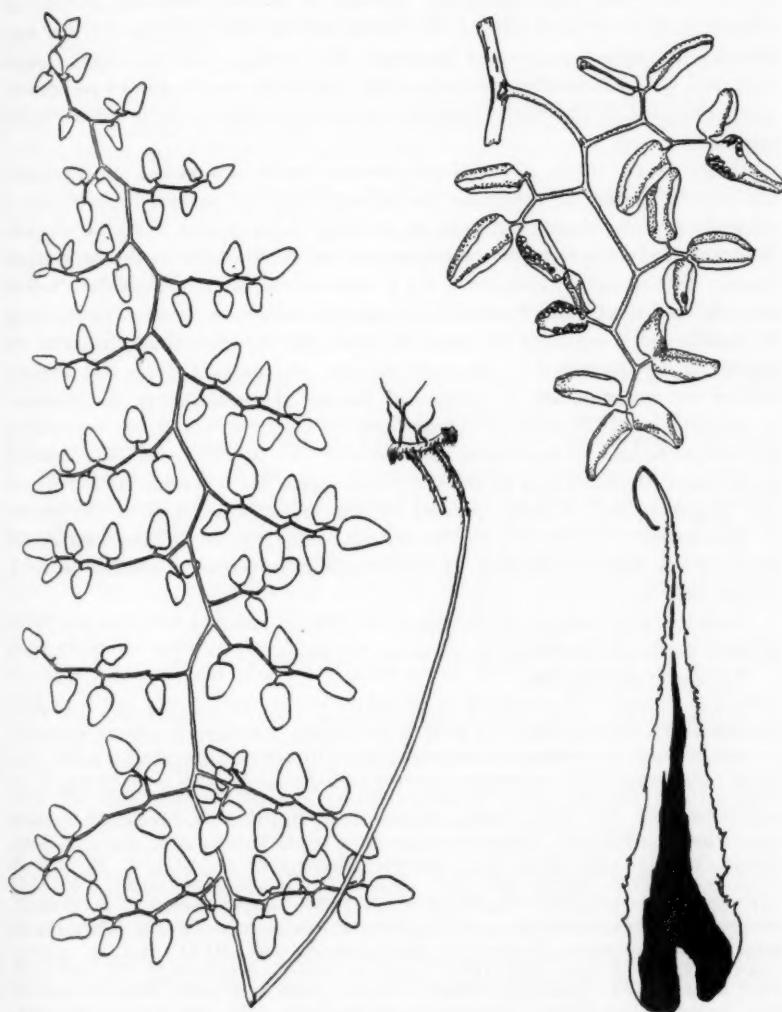


Fig. 11. *Pellaea ovata*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

the rachis strongly flexuous. Blade 15 cm. long and 2 cm. broad to 84 cm. long and 30 cm. broad, elongate-triangular, bi- to quadripinnate usually tripinnate, clear or grayish green, the pinnae descending at broad angles to the rachis, divided into 5 or more than 60 segments, long stalked, the pinna-rachises up to 14 cm. long, strongly flexuous. Segments 0.5 cm. long and 0.3 cm. broad to 4.5 cm. long and 2.5 cm. broad, ovate-triangular, sagittate or cordate, coriaceous, glabrous or sparsely pubescent, veins obscure, the border narrow, whitish lutescent, the apex obtuse or somewhat mucronate. Sporangia with stalks as long or slightly longer than the capsule, the annulus amber colored. Spores 32, occasionally 64 per sporangium, ellipsoidal or tetrahedral-globose, yellow with prominent light brown, rugose exospore.

These are the largest plants of the section, usually subscandent and unique in the retrorse position of the pinnae and strongly flexuous rachises. The species is relatively uniform throughout most of its range from central Texas to northern Argentina and appears to be the counterpart of *P. ternifolia* in the dark stiped group. Two species, *P. intermedia* and *P. andromedaefolia* at the northern end of its range and the Chilian *P. myrtillifolia* at the southern end, are related. As in *P. glabella* and *P. sagittata* the center of origin and direction of migration of the species can be determined by the spore number. In southern Texas and adjacent Mexico the specimens are 64 spored and produce the normal type of prothallia. A collection of R. M. & A. F. Tryon from Marble Falls, Texas, was reported by Dr. Britton to have a chromosome count of  $n = 29$ . South of this area extending to northern Argentina and in the Caribbean region the specimens are 32 spored and apogamous and evidently account for the general uniformity of the species.

Subscandent, in open sun, brushy savanna, among limestone rocks, on shaded banks, in oak forest, or growing on adobe walls, stone fences or crotches of trees, at 800–2850 m.

Southern Texas southward in Mexico and Central America to Nicaragua; Hispaniola; Venezuela southward to northern Argentina.

#### Representative specimens:

UNITED STATES. TEXAS: Correll 15230 (MO); E. Palmer 1428 (GH, MO, US, YU); Reverchon 1628 (F, GH, MO, US); R. M. & A. F. Tryon 5020 (GH, K, MEXU, MO, US). MEXICO. BAJA CALIFORNIA: Lemmon 145 (US). CHIAPAS: Ghiesbreght 204 (GH, US); Little & Sharp 9907 (US). CHIHUAHUA: Gentry 1538 (F, GH, MO, UC). COAHUILA: Wynd & Mueller 318 (GH, MO, US). DISTRITO FEDERAL: Lyonnnet 861 (GH, MO, NY, US). DURANGO: Ortega 5313 (US). GUANAJUATO: 1880, Duges (NY). GUERRERO: Hinton 11305 (F, GH, MO, US). HIDALGO: Chase 7217 (F, MO). JALISCO: Nov. 28, 1883, Pringle (F, UC), 5408 (MO, US). MEXICO: Hinton 7206 (F, MO); R. M. & A. F. Tryon 5134 (GH, K, MEXU, MO, US). MICHOACÁN: Arsène 3645 (MEXU, US), 9985 (GH, MO, US). MORELOS: Rose et al. 10193 (US). NUEVO LEÓN: C. H. & M. T. Mueller 1130 (F, GH). OAXACA: Conzatti & Makrinius 3030 (MEXU, US); Pringle 5951 (F, GH). PUEBLA: Arsène 1477 (US); Copeland 108 (MEXU, P, UC). QUERÉTARO: J. N. & J. S. Rose 11105 (US). SAN LUIS POTOSÍ: Schaffner 53 (P), 958 (GH, YU); R. M. & A. F. Tryon 5154 (MO). SONORA: Rose et al. 13113 (US). TAMAULIPAS: Bartlett 10313 (US). VERACRUZ: Bourgeau 3067 (GH, NY, P, UC, US, YU); Seaton 39 (F, GH, NY, US).

GUATEMALA: 1862, Godman & Salvin (BM); Hatch & Wilson 330 (UC, US); Standley 77095 (F, US); Steyermark 47282 (F, US).

HONDURAS: Standley 56496 (F, US). NICARAGUA: Standley 9721 (F), 10192 (F). COSTA RICA: Brade 199 (NY, UC), 16403 (P, US); Valerio 169 (US). HISPANIOLA. HAITI: Ekman H6153 (NY, US); Leonard 4804 (GH, NY, UC). DOMINICAN REPUBLIC: R. A. & E. S. Howard 8823 (GH, MO, NY, US).

VENEZUELA. Eggers 13417 (F, US); Pittier 7040 (GH, US). DISTRITO FEDERAL: Jahn 230 (US); 1929, Vogl (S-PA, UC). MÉRIDA: Fendler 89 (GH, MO, NY); Jahn 1082 (US).

COLOMBIA. VALLE: Cuatrecasas 20467 (F, US); Killip & Smith 16382 (GH, NY, US), 19090 (F, GH, US).

ECUADOR. Sept. 1918, Mille (S-PA), 131 (GH, US). AZUAY: Haught 3346 (GH, US). CHIMBORAZO: Camp 3167 (MO, US). IMBABURA: Mexia 7404 (F, UC, US); Wiggins 10270 (US). PICHINCHA: Asplund 6572 (US); Firmin 236 (NY, US).

PERU. APURÍMAC: Herrera 1497 (F, GH); Stork & Horton 10712 (F, UC). CUZCO: Cook & Gilbert 254 (US); Soukup 754 (F, GH); Vargas 1051 (GH, MO). HUÁNUCO: Sawada P108 (F). LORETO: Macbride 3142 (F, US).

BOLIVIA. April 1892, Kuntze (NY); Rusby 142 (NY, US). COCHABAMBA: Cardenas 3313 (F), 4798 (US); Janssen 70 (S-PA).

ARGENTINA. CATAMARCA: Oct. 1910, Castillon (GH). JUJUY: Aug. 1925, Cockerell (US); Eyerdam & Beetle 22417 (UC). TUCUMÁN: Borsini 13 (GH); Venturi 10367 (GH, MO, S-PA, US).

12. *Pellaea intermedia* Mett. ex Kuhn, in Linnaea 38:84. 1869. (Holotype: "Mexico, Herb. Fournier" B?). Fig. 12. Map 12.

*Pellaea intermedia* var. *pubescens* Mett. ex Kuhn, loc. cit. 1869. (Holotype: Wright Field no. 1190, Label no 825 B, Isotypes: GH! MO!).

*Cassebeera intermedia* (Mett. ex Kuhn) Farw. in Amer. Midl. Nat. 12:281. 1931.

*Pellaea intermedia* f. *pubescens* (Mett. ex Kuhn) Broun, Ind. N. Amer. Ferns, 132. 1938.

Rhizome slender, cord-like, dichotomously branched, long-creeping. Scales of the rhizome appressed, brownish, these and those of the base of the stipes bicolorous, elongate lanceolate-triangular, usually cordate, the sclerotic central portion usually lustrous (old scales sclerotic except for a narrow margin), straight or nearly so, the margins pectinate-serrulate, the cells short rectangular or with oblique end-walls, the apex filiform. Fronds 10 to more than 65 cm. long (largest specimens examined were incomplete), erect, straight and stiff, distant, monomorphic, the buds pubescent and with a few scales on the older portions of the rhizome as well as at the apex. Stipe and rachis convex or plane on the upper surface, more or less puberulent, straw colored to ruddy brown, becoming gray with age, the stipe breaking irregularly without articulation lines, the rachis straight or somewhat flexuous. Blade 8.0 cm. long and 3.5 cm. broad to 25 cm. long and 1.8 cm. broad, elongate-triangular, once pinnate to tripinnate, usually bipinnate, clear or grayish green, the pinnae at a broad angle to the rachis or slightly ascending, divided into 3–25 segments, long stalked, the pinna-rachises up to 10 cm. long, usually straight. Segments 0.5 cm. long and 0.3 cm. broad to 2.0 cm. long and 1.8 cm. broad, ovate to ellipsoidal, entire or ternate, coriaceous, glabrous, the veins obscure the borders narrow, whitish, the apex obtuse or somewhat mucronate. Sporangia with stalks as long or longer than the capsule, the annulus amber colored. Spores 32 or occasionally 64 per sporangium, ellipsoidal or tetrahedral-globose, yellowish with prominent tan or light brown, rugose exospore.

The choice of the name *P. intermedia* by Mettenius is of interest for he considered the species to be a hybrid between *P. sagittata* and *P. ovata*. This observation of the occurrence of a hybrid in nature is exceptional for that time. The closest relationship of *P. intermedia* as expressed in the form of the rhizome and leaves appears to be with *P. andromedaeifolia* and *P. ovata*.

Although the type of *P. intermedia* was not examined the pubescent variety is not maintained. All of the collections seen were somewhat pubescent and the

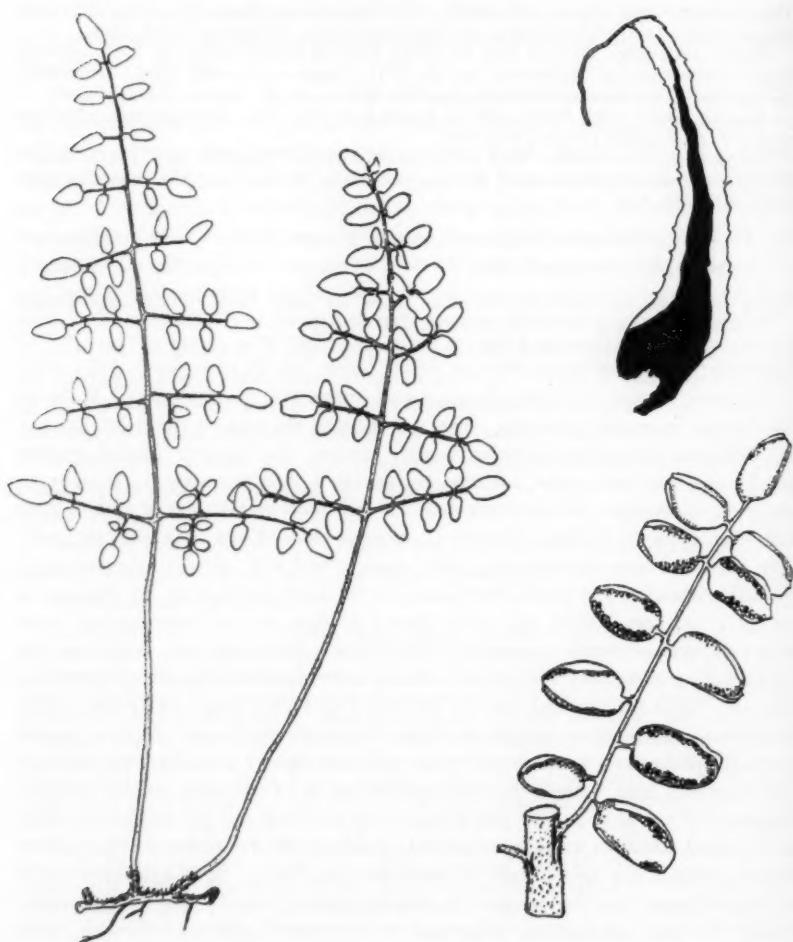


Fig. 12. *Pellaea intermedia*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

plants seem to become less so with age. Even though the type might be completely glabrous the single specimen would not validate the recognition of two varieties.

On shaded hillsides in oak humus or among limestone, porphyritic, or sandstone rocks, at 650–2400 m.

Trans-Pecos Texas to Arizona southward in Mexico to Zacatecas.

Representative specimens:

UNITED STATES. TEXAS: Mueller 8260 (GH, MO, NY, US); E. J. Palmer 34078 (MO, NY); R. M. & A. F. Tryon 5040 (GH, K, MO, US); C. Wright 825 (1190) (GH, MO). NEW MEXICO: Metcalfe 1177 (F, GH, US); Oct. 5, 1880, Rusby (F, GH, MO, NY, US, YU); Aug. 16, 1895, Wooton (GH, YU). ARIZONA: Blumer 1528 (F, GH, MO, NY, US); Goodding 770 (GH, US); Nov. 1, 1880, Greene (F, NY); Rotrock 494 (F, US), 674 (GH).

MEXICO. CHIHUAHUA: Pringle 461 (NY, US), 930 (MEXU, MO, NY, US). COAHUILA: Hinton 16700 (US); Johnston & Mueller 642 (GH), 859 (GH); E. Palmer 1426 (GH, US, YU), 1427 (GH, MO, US, YU); Stanford et al. 161 (GH, MEXU, NY, US), 354 (GH, MO, NY, US). NUEVO LEÓN: Mueller 1079 (GH); Taylor 84 (US). SONORA: White 330 (GH), 4743 (GH). ZACATECAS: Lloyd & Kirkwood 22 (MO), 135 (GH).

13. *Pellaea andromedaefolia* (Kaulf.) Féé, Gen. Fil. 129. 1850–52.

Fig. 13. Map 13.

*Pteris andromedaefolia* Kaulf. Enum. Fil. 188. 1824. (Holotype: Chamiso, Calif. P!, Photo: GH! US!).

*Allosorus andromedaefolius* (Kaulf.) Kze. in Linnaea 9:56. 1834.

*Platyloma andromedaefolia* (Kaulf.) J. Sm. in Journ. Bot. ed. W. J. Hooker 4:160. 1841.

*Cryptopteris divaricata* Nutt. ex Hook. Sp. Fil. 2:149. 1858, in synon.

*Cryptopteris pubescens* Nutt. ex Hook. loc. cit. 1858, in synon.

*Nothochlaena andromedaefolia* (Kaulf.) Keyserl. Polyp. Cyath. Herb. Bung. 29. 1873.

*Pellaea andromedaefolia* var. *pubescens* D.C. Eaton, Ferns N. Amer. 1:205. 1878, not properly of Baker, Syn. Fil. 150. 1868, which lists " $\beta$  C. *pubescens*".

*Pellaea andromedaefolia* var. *rubens* D.C. Eaton, in Bull. Torr. Bot. Club 6:360. 1879.

(Holotype: Mrs. S. P. Cooper, Santa Barbara, Calif. YU!).

*Pellaea rafaelensis* Moxley, in Amer. Fern Journ. 5:107. 1915. (Holotype: Moxley 214 LA, Photo: F! US!).

*Cassebeera andromedaefolia* (Kaulf.) Farw. in Amer. Midl. Nat. 12:280. 1931.

*Cassebeera andromedaefolia* var. *gracilis* Summers ex Farw. loc. cit. 281. 1931. (Holotype: Mrs. R. W. Summers, San Luis Obispo Co., Calif. MICH!).

*Cassebeera andromedaefolia* var. *pubescens* Farw. loc. cit. 281. 1931, nom. nud., based on "Cheilanthes pubescens Nutt."; evidently an attempted transfer of var. *pubescens* D.C. Eaton.

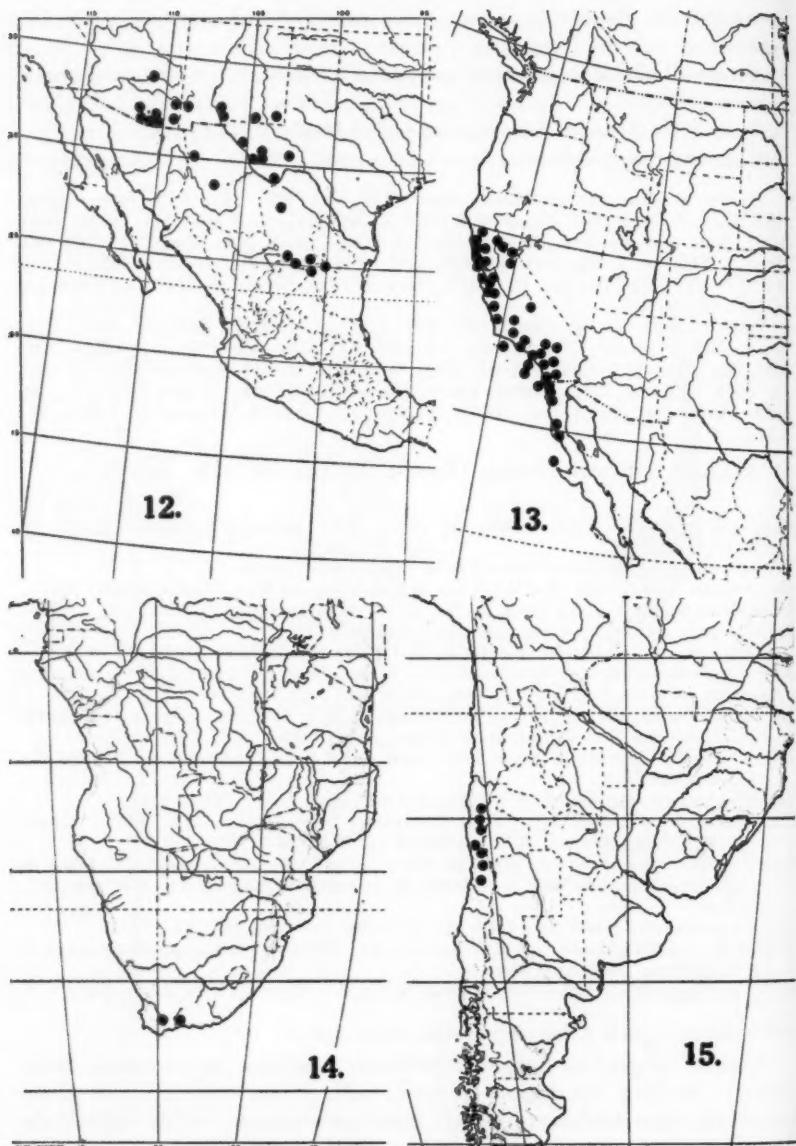
*Cassebeera andromedaefolia* var. *rubens* (D. C. Eaton) Farw. loc. cit. 281. 1931.

*Cheilanthes pubescens* Nutt. ex Farw. loc. cit. 281. 1931, in synon., apparently an error for "C[ryptopteris] pubescens" Nutt.

*Pellaea andromedaefolia* f. *gracilis* (Summers ex Farw.) Broun, Ind. N. Amer. Ferns 129. 1938.

*Pellaea andromedaefolia* f. *pubescens* (Eaton) Broun, loc. cit. 1938.

Rhizome slender, cord-like, dichotomously branched, long-creeping, rarely compact. Scales of the rhizome appressed, ruddy brown, these and those of the base of the stipes bicolorous, elongate lanceolate-triangular, usually cordate, the sclerotic central portion lustrous (old scales sclerotic except for a narrow margin), straight or nearly so, the margins pectinate-serrulate, the cells short-rectangular or



12. Distribution of *Pellaea intermedia*, 13. Distribution of *Pellaea andromedaefolia*, 14. Distribution of *Pellaea rufa*, 15. Distribution of *Pellaea myrtillifolia*.

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## TRYON—PELLAEA SECTION PELLAEA

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elongate with oblique end-walls, the apex filiform. Fronds 10–60 cm. long, erect, straight or nearly so, distant, rarely approximate, monomorphic, the buds paleaceous on older portions of the rhizome as well as the apex. Stipe and rachis convex or plane on the upper surface, glabrous, pubescent or paleaceous, straw colored to ruddy brown becoming gray with age, the stipe breaking irregularly without articulation lines, the rachis straight or somewhat flexuous. Blade 6 cm. long and



Fig. 13. *Pellaea andromedaefolia*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

3 cm. broad to 40 cm. long and 20 cm. broad, elongate-triangular, rhomboid or deltoid, bi- to quadripinnate, usually tripinnate, clear green or occasionally reddish, the pinnae usually ascending at a broad angle to the rachis, divided into 8 to more than 50 segments, long stalked, the pinna-rachises up to 14 cm. long, usually straight. Segments 0.2 cm. long and 0.1 cm. broad to 1.8 cm. long and 1.2 cm. broad, ellipsoidal or ovate, retuse, entire or ternate, herbaceous, glabrous or pubescent, veins evident, the borders narrow, whitish lutescent. Sporangia with short stalks usually less than one half the capsule length, the annulus amber colored. Spores 64 or 32 per sporangium, tetrahedral-globose or ellipsoidal, yellowish, with prominent tan or light brown, rugose exospore.

This species is closely allied to *P. intermedia*, *P. ovata* and an African species, *P. rufa*. They form a unique group characterized by reddish segments and the slender, dichotomously branching rhizome. A Chilian species is related to these on the form and color of the leaves and the form of the rhizome scales. The geographic pattern of the species of this group in the Americas is similar to that of other members of the section having a Cordilleran range. The alliance with *P. rufa* in the Karroo of South Africa, however, forms the only apparent link between the two main geographical centers of the genus *Pellaea*.

Most collections of *P. andromedaefolia* are glabrous and have 64-spored sporangia but plants from the southern part of the range are pubescent and have 32-spored sporangia. Both the 64 and 32 spored types have migrated to the coastal islands from the adjacent mainland. Cedrus Island off Baja California has the 32-spored plants while collections from more northerly islands, as Santa Catalina, Santa Cruz and San Clemente off the California coast, have 64 spores. The species is reported from southern Oregon on the basis of a single Howell collection from Roseburg, Douglas County. Since this collection is out of range and the spore number is not consistent with specimens from northern California the validity of the label may be questioned.

In dry, rocky ravines or ledges or along moist, shaded stream banks, at 60-1000 m.

**California and Baja California.**

**Representative specimens.**

UNITED STATES. CALIFORNIA: Abrams 3121 (GH, MO, NY, P, US); Abrams & Mc Gregor 30 (GH, NY, US); Abrams & Wiggins 350 (F, GH); Santa Barbara, Mrs. S. P. Cooper (YU); Copeland 2750 (GH, MO, NY); Eastwood 6378 (GH, NY, US); Fosberg R&3 (F, MO, NY), 676 (F, MO); Grant 918 (F, GH, MO, US); Hansen 656 (MO, P, US); Heller 4998 (US), 9014 (US); M. E. Jones 3227 (MO, NY, UC, US); Meyer 1371 (GH, MO); Nuttall 90 (F, US), 346 (F, US); E. Palmer 427 (F, GH, MO, NY); S. B. & W. F. Parish 513 (F, US); San Luis Obispo Co., Mrs. R. W. Summers (MICH); Torrey 595a (GH, NY); R. M. & A. F. Tryon 5064 (MO); Wiegand & Upton 2954a (F, MO, NY).

MEXICO. BAJA CALIFORNIA: April 16, 1936, Epling & Stewart (NY, US); E. Palmer 730 (NY, P, US), 749 (NY, US); Wiggins 5152 (US), 9967 (US).

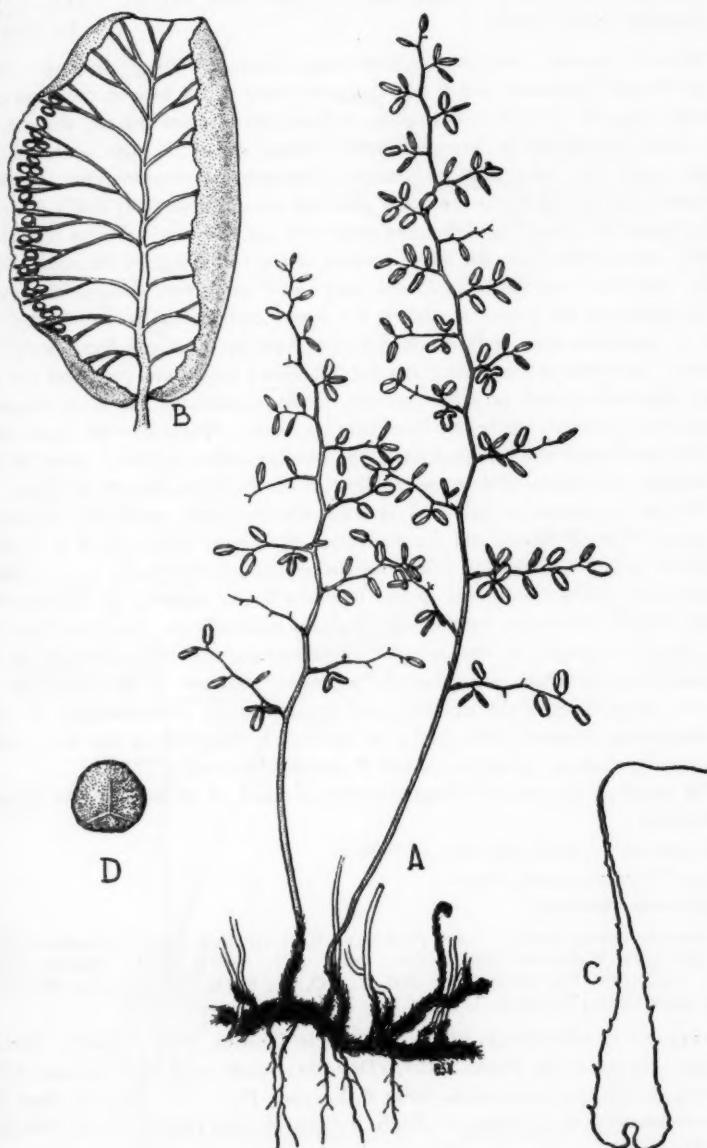


Fig. 14. *Pellaea rufa*, A, plant  $\times \frac{1}{4}$ ; B, segment with vein-ends exposed; C, rhizome scale; D, spore.

14. *Pellaea rufa* A. F. Tryon, Ann. Mo. Bot. Gard. 42:101. 1955. (Type: Compton 16402 US!). Fig. 14. Map 14.

Rhizome slender, cord-like, dichotomously branched, long creeping. Scales of the rhizome, appressed, ruddy tan, these and those of the base of the stipes concolorous, elongate, lanceolate-triangular, cordate, the margins sparsely dentate, the cells short-rectangular or elongate with oblique end-walls, the apex filiform. Fronds 12-40 cm. long, bent or straight, approximate, monomorphic, the buds paleaceous. Stipe and rachis convex or plane on the upper surface, nearly glabrous, ruddy tan to red becoming darker and gray with age, the stipe breaking irregularly without articulation lines, the upper portion of the rachis usually flexuous. Blade 10 cm. long and 2 cm. broad to 25 cm. long and 7 cm. broad, elongate-triangular, bi- to tripinnate, the pinnae ascending at a broad angle to the rachis, divided into 6 to 15 segments, long stalked, the pinna-rachises up to 4 cm. long, somewhat flexuous. Segments 0.3 cm. long and 0.2 cm. broad to 1.0 cm. long and 0.6 cm. broad, elliptical or oval or a few ternate, retuse, coriaceous, the veins immersed and obscure, glabrous, the border lutescent, crenulate. Sporangia with short stalks less than one-fourth the capsule length, the annulus amber colored. Spores 64 per sporangium, tetrahedral-globose, pale yellowish brown, with smooth exospore.

This species forms the only link between the two main geographic centers of the genus *Pellaea* in Africa and the Americas. It is most closely allied to *P. myrtillifolia* in central Chile and to *P. andromedaefolia* and *P. intermedia* in the western United States. The Cordilleran species *P. ovata* is also related. A characteristic reddish color of the stipes, rachises and segments especially on immature fronds in these species is unique in the section. Relationships are also expressed in the elongate-triangular form and generally tripinnate division of the blade, in the elliptical, retuse form of the segments and elongate basally cordate scales. *P. rufa* has concolorous rhizome scales similar to those of *P. myrtillifolia* but has a cord-like, creeping rhizome similar to that of *P. andromedaefolia*.

The range of the species is largely within a radius of 40 miles in the vicinity of Whitehill.

In crevices on rocky hillsides, at 1000 m.

Cape Province, South Africa.

Specimens examined:

UNION OF SOUTH AFRICA. CAPE PROVINCE: Rock crevices, Ngaap, Laingsburg Dist., Nov. 6, 1944, Compton 16402 (US), 2961 (K), 12619 (US); Dickson, Lady Barkly, recd. 5/75 (K); 1838, Drège (BM, K, MO, P); Rodin 3342 (UC, K, MO, US); Schelpe 4922 (MO, US), 4939 (US).

15. *Pellaea myrtillifolia* Mett. ex Kuhn in Linnaea 36:85. 1869. (Lectotype: Pöppig, Chile, Decbr. 1827, (Diar. 603) cited by Kunze, Linnaea 9:56. 1834, as *Allosorus andromedaefolius* B, Isotype: P!). Fig. 15. Map 15.

*Pellaea andromedaefolia* of authors not Kaulf., for example Gay, Hist. Fis. y Pol. Chile Bot. 6:493. 1853.

*Allosorus andromedaefolius* of authors not (Kaulf.) Kze., for example Sturm, Enum. Plant. Crypt. Vasc. Chile, 15. 1858.

*Allosorus myrtillifolius* (Mett. ex Kuhn) O. Ktze. Rev. Gen. Pl. 2:806. 1891.

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Fig. 15. *Pellaea myrtillifolia*, plant  $\times \frac{1}{2}$ ; pinna; rhizome scale.

Rhizome moderately stout to slender, compact or somewhat creeping. Scales of the rhizome spreading, tawny, ruddy brown, these and those of the base of the stipes concolorous, elongate lanceolate-triangular, cordate, the margins pectinate-serrulate with the base irregularly lobed, the cells short rectangular or elongate with oblique end-walls, the apex filiform, long attenuate. Fronds 14–50 cm. long, bent or straight, approximate, monomorphic, the buds pubescent with a few scales or nearly glabrous, evident only at the rhizome apex. Stipe and rachis convex or plane on the upper surface, sparsely pubescent, buff colored to reddish becoming gray with age, the stipe breaking irregularly without articulation lines, the rachis straight or especially the upper portion flexuous. Blade 9 cm. long and 4 cm. broad to 31 cm. long and 10 cm. broad, elongate-triangular or rhomboid, tri- or quadripinnate, clear green or reddish, the pinnae ascending, divided into 15 to more than 50 segments, long stalked, the pinna-rachises up to 8 cm. long, straight or slightly flexuous. Segments 0.2 cm. long and 0.1 cm. broad to 0.8 cm. long and 0.5 cm. broad, oval or ellipsoidal, retuse, usually ternate, coriaceous, glabrous, veins obscure, the border narrow lutescent. Sporangia with short stalks less than one fourth the capsule length, the annulus amber colored. Spores 64 per sporangium, tetrahedral-globose, yellow with prominent brown, rugose exospore.

Although endemic to Chile, the species is closely related to the group discussed under *P. rufa*. Geographically, it is closest to *P. ovata* in Peru and Argentina but morphological affinities as expressed in the structure and division of the leaves and the reddish color of the segments are closer to *P. andromedaefolia* in California.

An infusion of the plant is used in some parts of Chile to allay pain and thus the vernacular names *Coca* and *Yerba Coca* have been applied.

In rock fissures, at 1000–1400 m.

Central Chile.

Representative specimens:

**CHILE.** Cummings Herb. 184 (GH, K); Gay (CU, GH). ACONCAGUA: Bridges 557 (K). COQUIMBO: Pearce (K); Wagenknecht 18536 (MO, UC); Wagenknecht & Looser 4500 (GH). SANTIAGO: Dec. 7, 1923, Bebu (F); Claude-Joseph 632 (US), 897 (US); July 1934, Grandjot (MO); "Les Cruzes" Pöppig 84 (P).

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